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RESEARCH ARTICLE

Comparative survey of within-river genetic structure in Atlantic salmon; relevance for management and conservation

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Abstract In wild populations, defining the spatial scale at which management and conservation practices should focus remains challenging. In Atlantic salmon, compelling evidence suggests that genetic structure within rivers occurs, casting doubt on the underlying premise of the river-based management approach for this species. However, no comparisons of within-river genetic structure across different systems have been performed yet to assess the generality of this pattern. We compared the within-river genetic structure of four important salmon rivers in North America and evaluated the extent of genetic differentiation among their main tributaries. We found a hierarchical genetic structure at the river and tributary levels in most water systems, except in the Miramichi where panmixia could not be rejected. In the other cases, genetic differentiation between most tributaries was significant and could be as high as that found between rivers of the same geographical region. More importantly, the extent of genetic differentiation between tributaries varied greatly among water systems, from well differentiated (θ_{ST} = 0.035) to undifferentiated (θ_{ST} = −0.0003), underlying the difficulty in generalizing the ubiquity of within-river genetic structure in Atlantic salmon. Thus, this study underlines the importance of evaluating the genetic structure of Atlantic salmon in large water systems on a case by case basis in order to define the most appropriate spatial scale and focal unit for efficient management and conservation actions. The potential consequences of management at an inappropriate spatial scale are discussed.

Keywords Population structure · Genetic divergence · Management · Conservation · Salmon

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Introduction

Defining the spatial scale at which management and conservation practices should focus remains challenging, even for philopatric species with supposedly well-defined populations. For biological and practical reasons, the focal unit of conservation is often represented by the 'population', which, under the evolutionary paradigm, may be defined as a group of individuals of the same species living in close enough proximity that any member of the group can potentially mate with any other member (Hartl and Clark 1988; Waples and Gaggiotti 2006). Genetic data have long been used to identify population boundaries and orient conservation actions (e.g. Ryman and Utter 1987), but the constant development of new methodological and analytical approaches have contributed to an increasing use in recent years (Moritz 1994; Waples 1995; Fraser and Bernatchez 2001; Allendorf et al. 2004; Palsbøll et al. 2006; Schwartz et al. 2006; Waples and Gaggiotti 2006). For philopatric species, it may seem an easy task to define population boundaries and identify an appropriate focal unit of conservation because adults return to their natal site for reproduction, even after long distance migration. However, the geographical region associated with philopatry may vary in size and may be difficult to define precisely. Indeed, not all individuals are strictly philopatric in any given population and a certain rate of migration is

most often present and may vary among species and populations (Garant et al. 2007). Gene flow can then modify the size of the philopatric region associated with a population and influence the delimitation of an appropriate focal unit for conservation.

Anadromous Atlantic salmon, *Salmo salar*, is a long distance migratory and philopatric species that returns to spawn in its natal river after a feeding period at sea (Stabell 1984). Abundance of adult Atlantic salmon in North American rivers has been declining for several decades (Caron et al. 2005) and some, such as the Inner Bay of Fundy populations, have been identified as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, http://www.cosewic.gc.ca). This situation emphasizes the need to delineate genetic population structure precisely to help identifying appropriate focal units of conservation for this species. Genetic differentiation between rivers has been amply documented in Atlantic salmon (e.g. O'Reilly et al. 1996; Fontaine et al. 1997; McConnell et al. 1997; Spidle et al. 2003; Castric and Bernatchez 2004; Verspoor et al. 2005) and the river is generally considered as the spatial unit associated with a distinct salmon population. However, there is compelling evidence suggesting that significant genetic structure also occurs within large river systems in Atlantic salmon (Garant et al. 2000; Spidle 2001; Dillane et al. 2007; Vähä et al. 2007). This would suggest that philopatry and local adaptation could be present at a finer scale than that of the river (Vähä et al. 2008). However, comparison of within-river genetic structure in multiple water systems is needed to draw general conclusions and discuss the potential implications for conservation.

The main goal of this study was to document the genetic population structure of Atlantic salmon in large water systems located in different regions in eastern Canada. More specifically, the first objective was to describe and compare the within-river genetic structure of four important salmon rivers in North America: the Miramichi, the Restigouche, the Moisie and the Romaine water systems. The second objective was to evaluate the extent of genetic differentiation among tributaries and compare it to that commonly observed among rivers of the same geographical region. The final objective was to assess the generality of within-river genetic structure in Atlantic salmon and discuss the general implications for management and conservation.

Methods

Sampling

A total of 826 salmon were sampled in the main tributaries of four major water systems in eastern Canada: the Miramichi, the Restigouche, the Moisie and the Romaine (Fig. 1). An average of 64 salmon was collected per tributary in each water system (Table 1). Sampling of adult salmon occurred in the two main tributaries of the Miramichi water system, the Northwest (NO) and the Southwest (SO), using trap nets during summer 2004. In the Restigouche water system, sampling occurred using angling of adult salmon during summer 2004 in six important salmon tributaries: Matapédia (MA), Causapscal (CA), Patapédia (PA), Little Main (LM), Kedgwick (KE) and Upsalquitch (UP). In the Moisie water system, juvenile salmon (age 1+ and 2+) were sampled by electrofishing during summer 2005 at different sites in the three main tributaries: the Ouapetec (OU), the Nipissis (NI) and the main stem (MA). In the Romaine water system, juveniles (age 1+, 2+ and 3+) and adults were sampled in the two main tributaries, the Puyjalon (PU) and the main stem (MA), during the summers of 2001 and 2003 (Albert and Bernatchez 2006). Since no genetic differentiation was found between salmon sampled in different years in this system, temporal samples were pooled for the analyses (Albert and Bernatchez 2006).

River characteristics

The Miramichi water system located in the province of New-Brunswick has a watershed area of 14,000 km^2 and sustains the largest Atlantic salmon stock in North America with an annual estimated return of 54,000 adult salmon in 2000 (Chaput et al. 2001) and up to 82,000 in more recent years (G. Chaput, pers. comm., Department of Fisheries and Ocean Canada). One-sea-winter salmon, spending only one winter at sea before returning in freshwater for reproduction, represents approximately 73% of the adult returns in this system (G. Chaput, pers. comm., Department of Fisheries and Ocean Canada). The Restigouche water system is located at the boundary between the provinces of Québec and New-Brunswick and has a watershed area of approximately 10,000 km^2. Number of adults returning for reproduction has been estimated to be 8,859 with 10–75% being one-sea-winter salmon depending on the tributary (Caron et al. 2005). The Moisie and the Romaine water systems are located along the Mid North Shore of the Gulf of St. Lawrence, in the province of Québec, and their watershed areas extend over 19,200 and 14,350 km^2, respectively. Numbers of returning adults have been estimated to be 2,483 and 161 respectively and one-sea-winter salmon represents approximately 3% and 11% of the adult composition respectively (Caron et al. 2005). Stocking of juvenile salmon issued from native breeders has been reported sporadically in the Restigouche, mainly in the Kedgwick tributary between 1997 and 2001 (Ministère des Ressources Naturelles et de la Faune du Québec) and on a yearly basis in the Miramichi since multiple decades

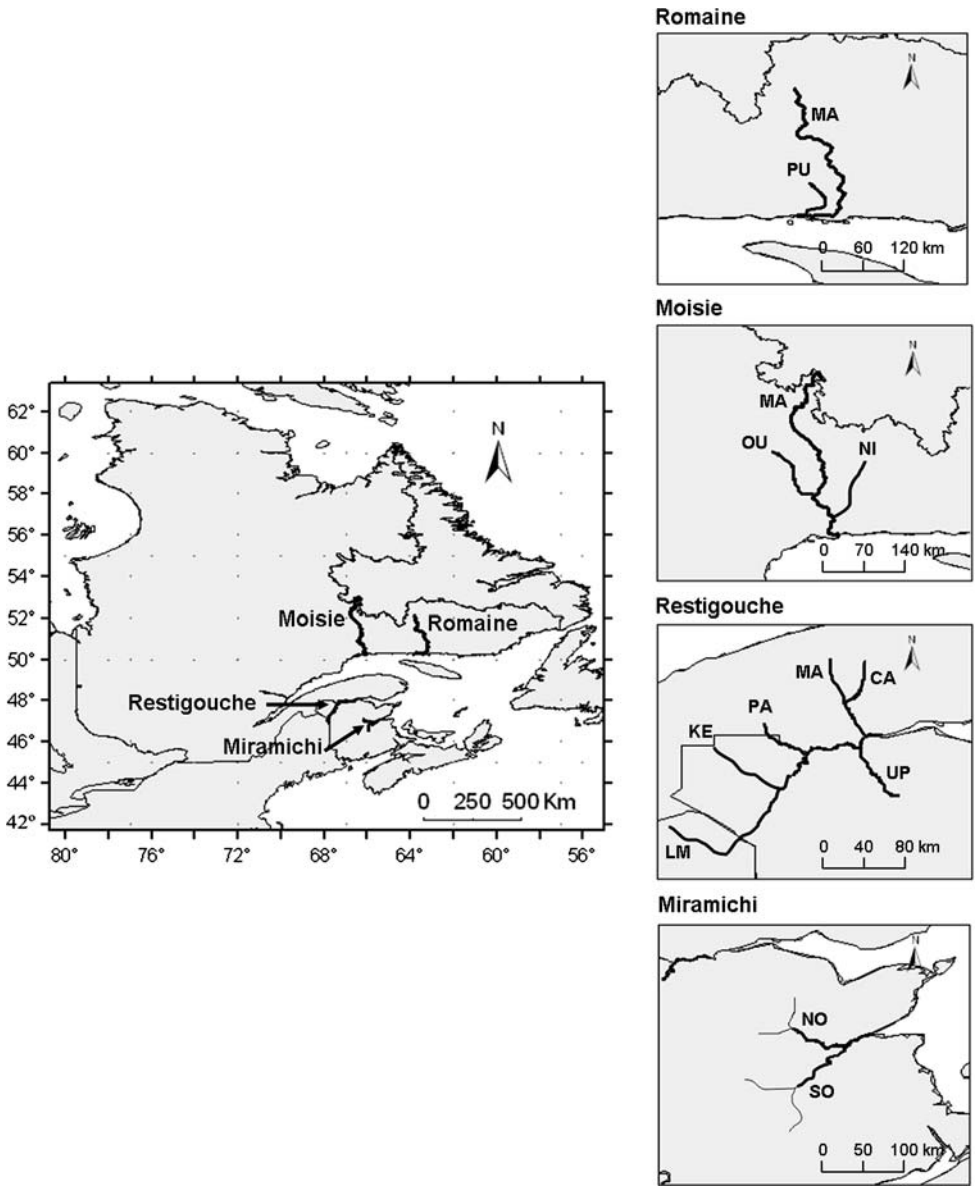

Fig. 1 Location of the four Atlantic salmon water systems in the provinces of Québec and New-Brunswick, Canada, analyzed in this study. Tributary codes are as in Table 1

(Chaput et al. 2001), but not in the Moisie or Romaine water systems.

Microsatellite genotyping

For each salmon, the adipose fin was clipped and stored in 95% ethanol, except for salmon sampled in the Romaine River where scales were extracted and used for genetic analysis. DNA was extracted from adipose fins or scales using the Qiagen DNeasy Tissue Kit following the guidelines of the manufacturer. Microsatellite polymorphism was quantified at 13 loci as detailed in the appendix of Dionne et al. (2007): *Ssa85*, *Ssa202*, *Ssa197* (O'Reilly et al. 1996), *Ssosl417* (Slettan et al. 1995), *SsaD85* (T. King unpublished), *SsaD71*, *SsaD144* (King et al. 2005), *MST-3* (Presa and Guyomard 1996), *Sssp1605*, *Sssp2210*, *Sssp2215*, *Sssp2216* and *SsspG7* (Paterson et al. 2004).

Statistical analyses

The potential occurrence of null alleles and scoring errors due to stuttering or large allele dropout in the data set was assessed using the software MICRO-CHECKER (van Oosterhout et al. 2004). The mean number of alleles (A) and the allelic richness (Ar), adjusted for the smallest tributary sample size (23 individuals), was calculated for each tributary using FSTAT 2.9.3.2 (Goudet 2001). Deviation from Hardy–Weinberg expectations and linkage disequilibrium were tested for each locus and for each tributary sampled using GENEPOP 3.4 (Raymond and Rousset 1995).

Table 1 Information and basic statistics associated with Atlantic salmon sampled in the tributaries of the Miramichi, Restigouche, Moisie and Romaine water systems. Water system and tributary codes are in parentheses. *N*: number of salmon sampled; He/Ho: expected and observed heterozygosity; A: mean number of alleles; Ar: allelic richness (number of alleles adjusted to the minimum sample size of 23 individuals); F_{IS}: inbreeding coefficient, values in bold are significantly different from zero

Water system	Tributary	Sampling year	Adult (*N*)	Juvenile (*N*)	Ho	He	A	Ar	F_{IS}
Miramichi (Mir)	Northwest (NO)	2004	109		0.84	0.88	21.0	14.5	**0.045**
	Southwest (SO)	2004	108		0.86	0.88	20.6	14.4	0.023
Restigouche (Res)	Causapscal (CA)	2004	50		0.90	0.87	15.8	12.6	−0.025
	Matapédia (MA)	2004	50		0.89	0.89	18.0	14.4	0.011
	Patapédia (PA)	2004	47		0.89	0.88	15.7	13.1	0.004
	Little Main (LM)	2004	61		0.86	0.89	17.5	13.9	**0.041**
	Kedgwick (KE)	2004	23		0.88	0.88	14.1	14.0	0.014
	Upsalquitch (UP)	2004	88		0.89	0.88	18.3	13.2	0.001
Moisie (MO)	Main (MA)	2005		66	0.87	0.87	15.5	12.3	0.010
	Nipissis (NI)	2005		46	0.86	0.86	14.6	12.5	0.013
	Ouapetec (OU)	2005		44	0.88	0.88	14.7	12.6	0.012
Romaine (RO)	Main (MA)	2001, 2003	10	50	0.87	0.84	13.4	10.6	−0.019
	Puyjalon (PU)	2001	25	50	0.81	0.84	15.3	11.6	**0.045**

Global allele frequency differentiation between pairs of tributaries within each river system was tested using the Fisher's exact test in GENEPOP 3.4 (Raymond and Rousset 1995). In order to evaluate the global proportion of the genetic variance associated with the genetic structure within as opposed to between water systems, an analysis of molecular variance (AMOVA) was conducted using ARLEQUIN 3.1 (Excoffier et al. 2005). This analysis was also conducted for each water system individually to compare the proportion of the variance found at the within-river genetic scale between water systems from different localities. The extent of genetic differentiation between tributaries in each water system was estimated using the F_{ST} estimator θ_{ST} (Weir and Cockerham 1984) in GENETIX 4.05.2 (Belkhir et al. 2000) and significance was assessed based on 1,000 permutations. Inbreeding coefficient F_{IS} was also calculated in this way, to test for potential family sampling artifact in juvenile samples (Allendorf-Phelps effect) compared to adult samples. Differences in allelic richness between tributaries and water systems were evaluated using a two-factor ANOVA (Water system and Tributary) on allelic richness per locus. Multiple pairwise-comparison tests using least-square means were performed for post-hoc comparisons, and a sequential Bonferroni correction was applied to evaluate significance (Rice 1989). Homogeneity of variances was tested using Cochran's *C*-test and normality of data was assessed by examining plots of the residuals. Genetic structure within water systems was finally illustrated using an unrooted neighbor-joining tree constructed based on Cavalli-Sforza and Edwards's (1967) chord distance (D_{CE}) in PHYLIP 3.66 (Felsenstein 2004). Consistency of tree topology was assessed by bootstrapping over loci for 1,000 pseudoreplicates using the SEQBOOT, GENDIST, NEIGHBOR and CONDENSE modules of the PHYLIP software and the tree was visualized in TREEVIEW 1.6.6 (Page 1996).

Results

Genetic polymorphism

No evidence for scoring errors due to stuttering or large allele dropout were found in the whole data set. Potential null alleles were suggested at only two tributary-loci combinations out of 169, with an estimated null allele frequency of 0.10 for *Ssosl417* in the Northwest Miramichi and 0.07 for *Sssp2210* in the main stem of the Moisie water system. We therefore concluded that neither potential null alleles nor scoring errors affected the outcome of the results. Deviations from Hardy–Weinberg equilibrium were identified in 10 out of 169 comparisons (all heterozygote deficits), a number close to the 8 significant tests expected by chance at $\alpha = 0.05$. There was no evidence of significant deviations associated with either particular loci or populations. No significant linkage disequilibrium was detected between pairs of loci for any population. In two previous studies conducted in the same geographic system (Dionne et al. 2007, 2008), the neutrality of each microsatellite locus was assessed using the LnRH neutrality test (Schlötterer 2002). The microsatellite *Sssp1605* was identified as a locus potentially under selection and was thus removed from further analyses. For salmon of the Romaine water system for which scales were used for DNA

extraction, the loci *Ssa85* and *MST-3* could not be amplified properly for many individuals and were discarded from the analyses. Mean allelic richness per water system, averaged over the remaining 10 microsatellites, ranged from 10.6 to 14.5 alleles, and observed heterozygosity was 0.87 on average (range: 0.81–0.90, Table 1). Inbreeding coefficients F_{IS} were small for all tributary samples and no evidence of family sampling artifact was found in the data set as juvenile samples did not show higher F_{IS} values than adult samples (*t*-test, $P = 0.44$). However, F_{IS} values were significantly different from zero in three tributary samples (Northwest Miramichi, Puylalon in the Romaine and Little Main in the Restigouche), and this could represent a plausible Wahlund effect where within-tributary genetic structure is present, as was found in the Puyjalon tributary (Albert and Bernatchez 2006).

Genetic differentiation

Allele frequency differences between tributaries were significant within the Romaine, Moisie and between most tributaries of the Restigouche water system (Table 2). However, according to global allele frequency differences, salmon from the Kedgwick tributary were not significantly differentiated from salmon of the Matapédia, Patapédia and Little Main tributaries in the Restigouche water system. Similarly, salmon from the two main tributaries of the Miramichi were not significantly differentiated according to allele frequencies. In the global AMOVA, a significant proportion of the variance was found between tributaries within water systems in general (1.14%, $P < 0.001$, Table 3). This proportion was only slightly lower than the proportion of the variance found among the four river systems (1.48%, $P < 0.001$). AMOVAs applied to each water system individually revealed that the proportion of the variance found between tributaries varied greatly among water systems from none in the Miramichi to 3.85% in the Romaine water system. The proportion of the variance between tributaries was intermediate for the Restigouche and the Moisie water systems (Table 3). The extent of genetic differentiation between pairs of tributaries (θ_{ST}) varied greatly among water systems and ranged from −0.0003 to 0.035 (Table 2). No genetic differentiation was found between the Northwest and Southwest tributaries of the Miramichi ($\theta_{ST} = -0.0003$). The extent of genetic differentiation was low to moderate between tributaries of the Restigouche ($\theta_{ST} = 0.0006$–0.020), and the Causapscal and Upsalquitch emerged as two significantly differentiated tributaries compared to all others (mean $\theta_{ST} = 0.016$ and 0.011 respectively). Tributaries of the Moisie were all significantly differentiated from each other ($\theta_{ST} = 0.010$–0.014) while those from the Romaine were the most genetically differentiated from all tributaries tested ($\theta_{ST} = 0.035$). Allelic richness did not differ between water systems nor between their respective tributaries (ANOVA: $P = 0.06$ and 0.99 respectively), although the former comparison was close to significance. The population tree was concordant with the genetic differentiation results. Tributaries from each water system generally clustered together with strong statistical support (Bootstrap: Romaine—99%, Moisie—91%, Miramichi—100%, Fig. 2), but this was less obvious for the Restigouche tributaries. The two samples from the Miramichi tightly clustered together with shorter branch lengths compared to other tributaries, illustrating the lack of significant genetic structure depicted in the above analyses. On the other hand, salmon of the

Table 2 Pairwise genetic differentiation (θ_{ST}) between Atlantic salmon sampled in tributaries of the Miramichi, Restigouche, Moisie and Romaine water systems (below diagonal). Above diagonal is the number of loci out of 10 significantly different under $\alpha = 0.05$ or after Bonferroni correction (number in parenthesis). Values in bold are not significantly different from zero globally. Values within squares represent comparisons between tributaries within water systems. See Table 1 for tributary codes

		Miramichi		Restigouche						Moisie			Romaine	
		NO	SO	CA	MA	PA	LM	KE	UP	MA	NI	OU	MA	PU
Miramichi	NO		**1(0)**											
	SO	**-0.0003**												
Restigouche	CA	0.020	0.021		3(2)	9(6)	9(7)	6(2)	9(7)					
	MA	0.009	0.010	0.008		3(0)	5(0)	**0(0)**	8(6)					
	PA	0.011	0.011	0.018	**0.004**		5(2)	**1(0)**	7(4)					
	LM	0.017	0.017	0.019	**0.004**	0.006		**1(0)**	10(8)					
	KE	0.014	0.014	0.017	**0.0006**	**0.003**	**0.002**		6(0)					
	UP	0.018	0.017	0.020	0.008	0.009	0.012	0.008						
Moisie	MA	0.019	0.019	0.032	0.014	0.012	0.012	0.017	0.018		7(5)	7(2)		
	NI	0.028	0.028	0.030	0.021	0.020	0.018	0.028	0.023	0.014		6(5)		
	OU	0.020	0.022	0.030	0.013	0.016	0.014	0.017	0.017	0.010	0.013			
Romaine	MA	0.046	0.048	0.052	0.039	0.032	0.042	0.033	0.040	0.042	0.050	0.041		10(10)
	PU	0.033	0.035	0.050	0.032	0.024	0.029	0.029	0.032	0.025	0.038	0.031	0.035	

Table 3 Global and individual analyses of molecular variance (AMOVA), partitioning genetic variance between individual Atlantic salmon, between tributaries within water systems and between the four water systems

	Source of variation	d.f.	% Variance	*P*
Global	Among rivers	3	1.48	<0.001
	Among tributaries within rivers	9	1.14	<0.001
	Among individuals within tributaries	1,635	97.39	<0.001
Miramichi	Among tributaries within rivers	1	−0.02	0.61
	Among individuals within tributaries	432	100.02	
Restigouche	Among tributaries within rivers	5	1.04	<0.001
	Among individuals within tributaries	630	98.96	
Moisie	Among tributaries within rivers	2	0.93	<0.001
	Among individuals within tributaries	309	99.07	
Romaine	Among tributaries within rivers	1	3.85	<0.001
	Among individuals within tributaries	264	96.15	

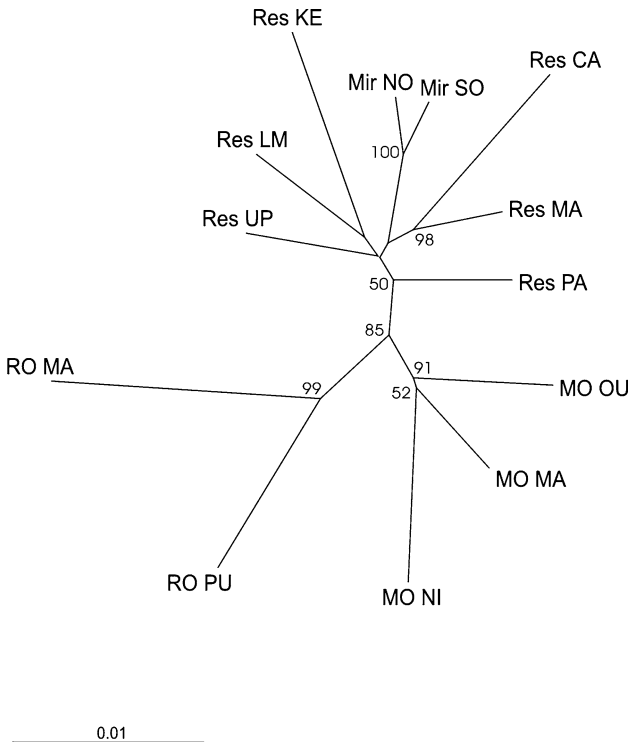

Fig. 2 Atlantic salmon population tree based on Cavalli-Sforza and Edwards's (1967) chord distance (D_{CE}) calculated using 10 microsatellite markers. Bootstrap values over 50 are shown. Water system and tributary codes are as in Table 1

Romaine tributaries were associated with longer branch lengths compared to all others, illustrating the higher genetic differentiation between these salmon groups.

Discussion

Our main objective was to document and compare the within-river genetic structure of four important salmon rivers in North America. Genetic differentiation was found between tributaries of most water systems and represented a significant but slightly smaller proportion of the variance than that found among water systems. Within-river genetic structure in Atlantic salmon was also previously reported elsewhere, such as in the Sainte-Marguerite River in Canada (Garant et al. 2000; Landry and Bernatchez 2001), between two tributaries of the Moy system in Ireland (Dillane et al. 2007), in the Varzuga River in Russia (Primmer et al. 2006), in the Teno River in northern Europe (Vähä et al. 2007, 2008) and within the Penobscot River drainage in Maine (Spidle 2001). This indicated that significant genetic structure of Atlantic salmon within relatively large water systems is not uncommon. Significant structuring based on allozymes has also been observed within certain rivers in Europe (reviewed in Verspoor et al. 2005, but see Jordan et al. 1992). However, no comparisons of the extent of within-river genetic structure across different systems have yet been performed. Here, the extent of genetic differentiation between tributaries varied from well differentiated in the Romaine and the Moisie, moderately differentiated in the Restigouche, to undifferentiated in the Miramichi water system. Moreover, the extent of genetic differentiation between tributaries was sometimes as high as that observed between rivers of the same geographical region. Indeed, the proportion of the variance captured in the AMOVA was similar among and within rivers. Moreover, genetic differentiation among North Shore rivers and among Southern Québec rivers averaged θ_{ST} = 0.027 ± 0.017 and θ_{ST} = 0.011 ± 0.0009, respectively (using the same loci for calculation, Dionne et al. 2008). These values are close to the mean θ_{ST} observed between tributaries of the northern and southern water systems in this study (northern: θ_{ST} Moisie and Romaine = 0.012 and 0.035; southern: θ_{ST} Restigouche and Miramichi = 0.009 and −0.0003).

Quite surprisingly, the large Miramichi water system differed from the others in that no significant genetic differentiation between its two main tributaries was detected.

Similarly, no significant genetic differentiation was observed between early and late spawning runs in this system or between salmon from the river mouth and those from Clearwater Brook, a tributary of the Southwest Miramichi (Dodson and Colombani 1997). This lack of genetic structure also corroborated previous tagging studies which revealed significant straying in multiple cohorts whereby tagged individuals born in one tributary returned to the other as adult for reproduction (Kerswill 1971; Chaput et al. 2001). Indeed, straying between the two tributaries was recently estimated to range between 16.3% and 21.0% (Chaput et al. 2001). It is then possible that the large population size and the high dispersal rate translated in low genetic drift and high gene flow between tributaries and prevented genetic differentiation to establish. Returns of hatchery stocked salmon represent in general less than 1% of the total returns in this system (Chaput et al. 2001), which can be predicted to have a much lower impact than straying on genetic structure homogenization. Genetic structure was also verified within the Northwest and the Southwest tributaries using STRUCTURE 2.1 (Pritchard et al. 2000) and no sub-structure could be detected in either tributary. Indeed, the highest probability was obtained with $K = 1$ population and decreased for a higher number of populations for each tributary analysis (data not shown). However, the genetic structure deeper in the system can only be adequately described by a thorough sampling of smaller tributaries. This lack of genetic differentiation between the two main tributaries of the Miramichi contrasts, however, with the heterogeneity observed at two out of eight polymorphic protein-coding loci between different samples of the Southwest branch (Ståhl 1987). Variation in transferrin allele frequency *TF*A* was also observed within the Miramichi water system based on fish sampled in 1969–1970 (0.222–0.479, Møller 2005). However, it remained unclear if this variation was strictly due to population structure, random variation or sampling artifact as the number of fish sampled at each site was not stated and no statistical tests were conducted between each pair of samples to evaluate the significance of that differentiation. It is noteworthy, however, that although no genetic differentiation was found at microsatellites, this does not exclude the possibility of within-river differentiation at adaptive genes.

We found that genetic diversity was comparable among water systems and their respective tributaries. The absence of major differences in genetic diversity between tributaries contrasted with a recent study conducted in the Teno River system in northern Europe where salmon from the main tributary showed a higher level of genetic diversity than those from adjacent tributaries (Vähä et al. 2007). Our results suggest that these recent findings cannot be taken as a rule for all Atlantic salmon water systems, at least not in eastern Canada. Temporal genetic variation was also evaluated in a previous study on six rivers in eastern Canada, including the Causapscal and the main tributary of the Moisie water system, and no significant genetic differentiation was found between temporal replicates (Dionne et al. 2008). We then assume that the genetic structure observed in this study is relatively stable over a short time period. Stable genetic structure among populations in the Saguenay region, Québec, further suggested that stability can be observed over several generations in Atlantic salmon (Tessier and Bernatchez 1999).

The general pattern we observed whereby a lack of structuring was found between the two main tributaries of the largest river system (Miramichi River) and a pronounced genetic subdivision was observed in the smallest population of the Romaine River contrasted with the patterns reported in European brown trout (*Salmo trutta*) populations. Indeed, genetic structure of certain large brown trout populations better supported a member-vagrant model (Hansen et al. 2002) where a strong and stable genetic structure potentially evolved as a result of precise homing in appropriate spawning areas (Sinclair 1988; Sinclair and Iles 1988). Genetic structure of some smaller populations, however, better supported a metapopulation model where fluctuations in population sizes as well as local extinctions and recolonizations lead to weaker and unstable genetic structure (Østergaard et al. 2003). In Atlantic salmon, smaller populations harbored the strongest within-river genetic structure which contrasted with a metapopulation model but better supported the predominant influence of genetic drift. To shed further light on these aspects, within-river genetic structure should be compared in different systems over multiple generations. Overall, even though within-river genetic structure can be of the same magnitude as that observed between rivers of the same geographical location, the extent of genetic differentiation between tributaries cannot be generalized across all water systems. This study then underlines the importance of evaluating the genetic structure of each large water system individually for management and conservation purposes.

The management of Atlantic salmon rivers in eastern Canada is generally conducted at the regional or at the river scale such as in the province of Québec (Caron et al. 2005). A river-based approach assumes that a population is defined at the scale of the river and that the precision of homing and natal site fidelity is occurring at that spatial scale. However, this study showed that for large water systems, within-river genetic structure is a possible biological reality, further suggesting that site fidelity might occur at least at the tributary scale and/or that local adaptation might develop at a finer scale than that of the river (Garant et al. 2000; Landry and Bernatchez 2001; Vähä

et al. 2008). Indeed, local adaptation of Atlantic salmon was shown to be an important evolutionary process at the scale of the river (Dionne et al. 2007) and evidence exists that this could also be the case at a finer scale (see reviews in Taylor 1991; Garcia de Leaniz et al. 2007), such as conceptually demonstrated in multiple tributaries of the Teno River (Vähä et al. 2008).

Potential risks associated with management at an inappropriate spatial scale: implications for conservation

What then may be the consequences of managing Atlantic salmon at an inappropriate scale (summarized in Table 4)? First, if within-river genetic structure exists but a river-based management approach is still prioritized, one would assume that census and effective population sizes would be much larger than the actual population size of the tributary. Effective population size is considered as a parameter of prime importance for the prediction of a population's capacity to survive in a changing environment (Caballero 1994; Nunney 1999; Frankham et al. 2002; Frankham 2005; Pertoldi et al. 2007). One risk would then be to assume that the river-population would be protected relatively well against environmental changes over evolutionary time while in reality tributary-populations would be more susceptible to stochastic fluctuations in the environment and more susceptible to lose genetic diversity through the marked influence of genetic drift in small populations (Frankham et al. 2002; Frankham 2005). This would then lead to an underestimation of extinction risks. However, the magnitude of this discrepancy would be mitigated by the degree of connectivity between tributaries and other rivers, with high gene flow maintaining genetic variation and decreasing the influence of stochastic fluctuations and genetic drift (Frankham et al. 2002; Lenormand 2002). Another risk in considering one river as a manageable population while internal genetic structure exists would be to amplify the importance of gene flow between tributaries while in reality salmon in different tributaries may be much more ecologically and evolutionarily isolated. This would imply that the loss of salmon from one tributary, due to some human activities for example, would be more difficult to restore than predicted under the river-based management approach. Another non-exclusive risk would be to ignore the importance of local adaptation at a fine scale that may allow the persistence of groups of individuals within rivers. Indeed, certain genotypes can translate into higher individual fitness and be potentially optimal in certain environments (Kawecki and Ebert 2004), representing the potential for local adaptation at a fine spatial scale in the wild. In Atlantic salmon, multiple heritable morphological and life history traits such as body size and age at maturity, as well as allele frequencies at the Major Histocompatibility Complex (MHC) class II gene involved in pathogen resistance, have been shown to vary within a river system, a pattern that may represent adaptation at a fine spatial scale (Landry and Bernatchez 2001; Aubin-Horth et al. 2005, 2006). If this is the case, conservation of these differences would allow the

Table 4 Summary of the potential risks associated with management at an inappropriate spatial scale. See text for further details. Ok indicates management at an appropriate spatial scale

	Within-river genetic structure	
	No	Yes
Management spatial scale		
River	Ok	Underestimates impacts of stochastic fluctuations
		Underestimates risks of lost of genetic diversity through genetic drift
		Underestimates extinction risks
		Overestimates gene flow between tributaries
		Ignores fine scale local adaptation
		Underestimates fishing impacts
		Risks of homogenization through stocking practices
		Risks of overfishing specific populations
Tributary	Unnecessary proliferation of management actions	Ok
	Underestimates gene flow between tributaries	
	Ignores potential impacts of management actions on the entire system	

maintenance of the potential for local adaptation and population persistence, processes that would be hampered by a river-based management approach. For example, stocking practices often consist in sub-sampling adults in a specific river locality to eventually spread the progeny over the whole river system. Fishing impact can also be underestimated when internal genetic structure exists as harvesting occurs in a smaller than expected pool of individuals. Also, when fishing is spatially segregated, higher pressure can be exerted on some populations more than others (e.g. Potvin and Bernatchez 2001). Within-river genetic structure when detected could then help to better orient these management practices.

Conversely, assuming significant intra-river genetic structure when there is none would lead to the unnecessary proliferation of management actions and, more seriously, to underestimating the role of gene flow in insuring connectivity between tributaries and its importance in the persistence of the whole-river population. From a conservation point of view, this would then ignore that a management action in one tributary could have major influences on the evolution of salmon of other tributaries in the same water system. In a genetically homogeneous system, coordination of management plans should then be emphasized to promote efficient Atlantic salmon conservation. Overall, the potential risks and inherent costs associated with management at an inappropriate spatial scale underline the need to integrate genetic monitoring into traditional monitoring approaches, in order to gain information on the scale of the genetic structure and the temporal stability associated with each manageable system. Genetic monitoring can provide relevant ecological and evolutionary information, often unavailable using other approaches (Schwartz et al. 2006), that could help in defining conservation priorities.

In conclusion, this study highlighted the existence of a hierarchical genetic structure in Atlantic salmon at the river and tributary scales in most water systems, except for the Miramichi. Genetic differentiation between salmon from different tributaries can be as high as that observed between rivers of the same geographical region. However, the extent of genetic differentiation between tributaries varied greatly among rivers, from well differentiated to undifferentiated, underlying the uniqueness of each large water system in terms of population dynamics and evolution. Finally, this study underlines the importance of integrating genetic monitoring and choosing the appropriate spatial scale for managing Atlantic salmon populations in order to promote efficient conservation actions.

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