

Lacustrine spatial distribution of landlocked Atlantic salmon populations assessed across generations by multilocus individual assignment and mixed-stock analyses

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Abstract

The objective of this study was to assess the spatiotemporal distribution of four landlocked Atlantic salmon (*Salmo salar*) populations during their sympatric feeding phase in lake St-Jean (Québec, Canada). A total of 1100 fish captured over a period of 25 years was genotyped at six microsatellite loci in order to assess the temporal stability of the relative proportion of each population in different lake sectors using both individual-based assignment and mixed-stock analysis. Estimates of relative proportions obtained from both methods were highly correlated. A nonrandom spatial distribution of populations was observed for each period and, despite the fact that the overall proportion of each population varied over time, the pattern of differential distribution remained generally stable over time. Furthermore, there were indications that the extent of horizontal spatial overlap among populations was negatively correlated with that of their genetic differentiation at both microsatellites and a major histocompatibility complex locus, and independent of the geographical distance between the rivers of origin. We discuss the hypothesis that the temporal stability of spatial distribution, the lack of an association between spatial partitioning and geographical distance between rivers of origin, and the apparent negative correlation between spatial overlap and genetic differentiation, reflect the outcome of selective pressures driving behavioural differences for spatial niche partitioning among populations.

Keywords: Atlantic salmon, microsatellite, multilocus genotype, niche partitioning, population assignment, *Salmo salar*

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Introduction

A common biological feature of north temperate lakes is the occurrence of recently diverged sympatric fish populations, which are referred to as ecotypes, morphs or forms (reviewed in Taylor 1999). Typically, these differ in patterns of morphological, behavioural and life history traits that are associated with specializations for differentially exploiting benthic and limnetic prey (Schluter & McPhail 1993). This has led to the general recognition that resource-based natural selection is the primary force driving the divergence and reproductive isolation of these populations (Skúlason & Smith 1995; Robinson & Schluter 2000).

Less attention has been paid to the existence of lacustrine sympatric fish populations that do not fit the general pattern of limnetic–benthic dichotomy of trophic specialization. Yet, investigation into such situations is of particular interest as they raise the hypothesis that ecological axes, other than alternative trophic resources, may also play a role in promoting divergence and the sympatric occurrence of fish populations in north temperate lakes. For example, Taylor *et al.* (1997) documented the sympatric existence of two reproductive ecotypes of kokanee (*Oncorhynchus nerka*) that could not be distinguished morphologically, sharing a common limnetic habitat and feeding niche as juveniles. Lack of trophic niche partitioning during the sympatric lacustrine phase of their life cycle has also been reported between anadromous and resident ecotypes of the same species (Wood *et al.* 1999). Turgeon *et al.* (1999) also reported a lack of association between morphological specialization and trophic use among four

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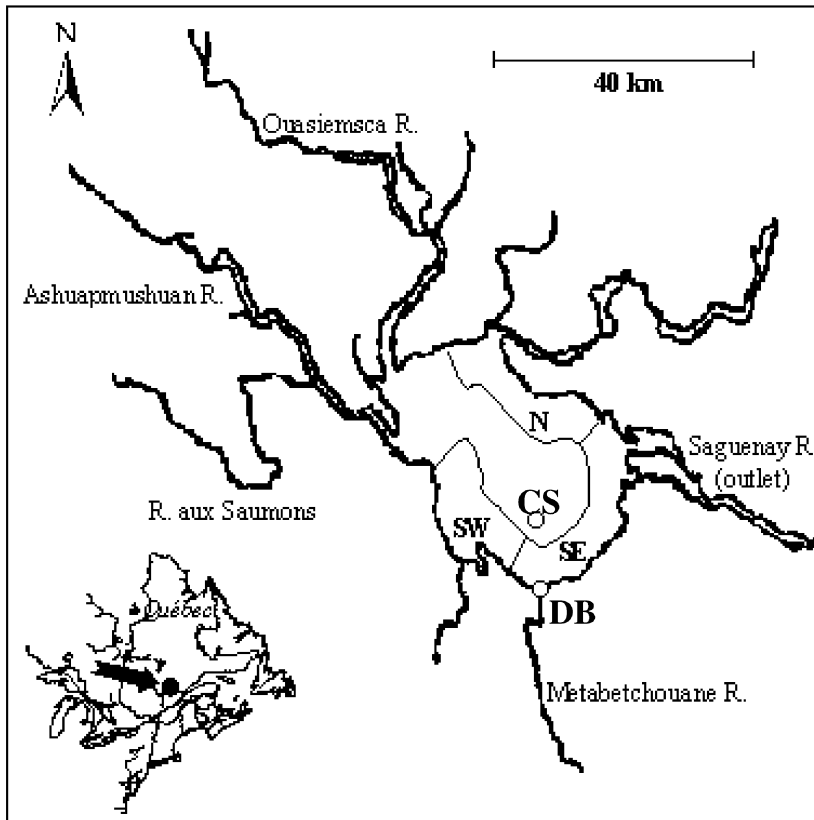


Fig. 1 Location map of Lake St-Jean (lower left corner), and its tributaries, and definition of the sectors analysed in this study. SW, south-west; SE, south-east; N, north; CS, central sector; DB, Desbiens' Bay (the latter two represented by empty circles).

sympatric morphotypes of ciscoes (*Coregonus* sp.), which revealed a more pronounced pattern of epibenthic niche partitioning based on bottom depth rather than limnetic vs. benthic habitat or diet.

We recently documented the sympatric occurrence of four genetically distinct populations of ouananiche, the resident lacustrine form of Atlantic salmon (*Salmo salar* L.) in Lake St-Jean, a large (1100 km²) but shallow lake (mean depth of 11 m), located in central Québec, Canada (72°00' W, 48°40' N; Fig. 1) (Tessier *et al.* 1997; Tessier & Bernatchez 1999). These populations reproduce in four different tributaries of the lake: Rivière-aux-Saumons, Ashuapmushuan, Métabetchouane and Ouasiemscas rivers (Fig. 1). Juveniles spend 2–3 years in tributaries before migrating down to the lacustrine feeding grounds where fish from the different populations may potentially mix. Sexually mature fish return to their natal river after 2–4 years to complete their life cycle. No obvious morphological differences characterize fish from different populations (Michel Legault, Société Faune et Parcs du Québec, personal communication). Similarly, there is no evidence for trophic resource partitioning in terms of benthic–limnetic prey, as all salmon appear to be pelagic piscivores, the rainbow smelt (*Osmerus mordax*) composing up to 75% of their diet (Nadon 1991). Consequently, niche

partitioning among these populations, if any, may be more likely to occur spatially on the horizontal axis than on the vertical axis, or limnetic/benthic habitats. A first objective of this study was therefore to test the null hypothesis of homogeneity in the horizontal distribution of relative proportions of the four sympatric salmon populations in lake St-Jean.

Tessier *et al.* (1997) reported that the extent of genetic differentiation based on microsatellite loci was highly variable among these populations, a pattern also confirmed recently by analysis of the major histocompatibility complex (MHC; Landry & Bernatchez, 2001). Of particular interest were the observations that: (i) gene flow between the Métabetchouane population and its colleagues was much more restricted than reported among anadromous Atlantic salmon populations over a much larger geographical scale; and (ii) the genetic differentiation between the Ashuapmushuan population and that of its tributary, Rivière-aux-Saumons, was more pronounced than that observed between the Ashuapmushuan and the neighbouring Ouasiemscas river population. These observations raised the hypothesis that the pattern of gene flow among these salmon populations may have been shaped by factors other than the probability of straying related to geographical distance among rivers of origin (discussed

in Tessier *et al.* 1997). Namely, Bernatchez *et al.* (1999) recently hypothesized that the variable extent gene flow among sympatric populations could be a consequence of directional selective pressures promoting population-specific specializations for sharing ecological niches in sympatry (see details in Discussion). This hypothesis has recently been supported by a negative correlation between the extent of gene flow occurring between sympatric ecotypes of the lake whitefish (*Coregonus clupeaformis*) and that of their morphological trophic specialization. This indicated that the extent of their reproductive isolation may be driven mainly by resource-based divergent selection in different environments (Lu & Bernatchez 1999). A similar pattern has subsequently been reported in four sympatric ecotypes of the Arctic charr (*Salvelinus alpinus*) (Gíslason *et al.* 1999). In this context, a second specific objective of this study was to test the null hypothesis of no correlation between the extent of genetic differentiation and that of horizontal spatial overlap among salmon populations.

In the absence of reliable phenotypic identifiers, estimating the spatial distribution of populations can best be achieved by genetic identification (Olsen *et al.* 2000). As such, the quantification of proportions of the four populations in different sectors of the lake closely parallels the problem of genetic stock identification (GSI) in mixed fisheries [also called mixed-stock analysis (MSA)]. In brief, allelic frequencies are first determined in all populations potentially contributing to the mixed fishery. The most likely proportions of each population in the mixed fishery are then determined based on the maximum likelihood of allelic composition of the mix, given allelic frequencies in baseline populations. GSI has been achieved successfully using allozyme or microsatellite markers, particularly in Pacific salmonids (Fournier *et al.* 1984; Beacham *et al.* 1987; Wood *et al.* 1987; Utter & Ryman 1993; Scribner *et al.* 1998; Beacham & Wood 1999; Seeb & Crane 1999; Shaklee *et al.* 1999).

The availability of highly variable genetic markers (e.g. microsatellite loci) now allows the definition of individual multilocus genotypes, and opens exciting avenues of research and applications (Estoup & Angers 1998; Davies *et al.* 1999). Namely, assignment of an individual to its most probable population of origin has been shown to have a diverse range of applications (Paetkau *et al.* 1995; Nielsen *et al.* 1997; Palsbøll *et al.* 1997; Waser & Strobeck 1998; Roques *et al.* 1999; Primmer *et al.* 2000). A number of studies has applied individual population assignment methods in fishes (Nielsen *et al.* 1997, 1999a,b; Estoup *et al.* 1998; Roques *et al.* 1999; Olsen *et al.* 2000; Primmer *et al.* 2000). To our knowledge, however, none has used it to quantify admixture proportions of fish populations in a sample of individuals of unknown origin *per se*. A third objective of this study was therefore to compare the estimates of

relative contribution based on individual multilocus genotype identification with those obtained using the more widely applied GSI method.

Materials and methods

Mixed samples of unknown origins

Given the social importance of the ouananiche in Lake St-Jean, intensive collection using invasive sampling gear (e.g. gill-nets) was ethically impossible. Consequently, scale samples were obtained from recreational fishing catches, which have traditionally been collected by governmental agencies using the same protocol over the last 25 years. Although this method may potentially imply selective sampling (as with most fishing gear), it offers the advantage of standardizing the sampling design over time. Our sampling aimed to quantify the relative proportion of the four populations in three sectors defined historically for management purposes; south-east, south-west and north (Fig. 1). Uncovered coastal areas are characterized by a shallow, warm-water habitat unsuitable for salmon, and the central part of the lake has traditionally not been exploited by fishermen, mainly because of its remoteness. In order to assess the temporal stability of the population distribution, the relative proportion of the four populations in these sectors was quantified for three different periods: 1970s, 1980s and 1990s. For each period, samples from two (three for the 1990s) consecutive years were analysed to also test for within-period stability. For each year, samples were distributed evenly over the fishing season (from early June to mid-September), and the three fishing sectors. Forty-nine fish collected in 1999 ($n = 36$) and 2000 ($n = 13$) from the traditionally unexploited centre of the lake, and 103 fish angled in Desbiens' bay during the 1970s were added to the analysis. A total of 1100 fish was thus analysed in this study. Details of sample sizes for mixed samples are given in Table 1.

Table 1 Sample sizes for mixed samples in the three main sectors sampled for three time periods. N; north sector, SE; south-east sector, SW; south-west sector

Period	Year	Total	Numbers by sector		
			N	SE	SW
1970s	1975	92	31	28	33
	1976	266	93	92	81
1980s	1986	241	64	87	90
	1987	86	17	35	34
1990s	1994	54	13	29	12
	1995	76	26	19	31
	1996	133	47	42	44

Baseline data set

The data set for baseline populations was obtained from Tessier *et al.* (1997) and Tessier & Bernatchez (1999, 2000). In these studies, ≈ 40 adult salmon from each of four populations were captured during their spawning migration and analysed using the same microsatellites as here for each of two periods covering the same time span as this study. None of these samples deviated significantly from Hardy–Weinberg equilibrium (HWE), and no linkage disequilibrium was detected. Details of these analyses can be found in these studies as well. Both individual population assignment and MSA methods require accurate estimates of allele frequency distribution for all baseline populations. As mentioned by Waples (1998), the analysis of temporal replicates represents the best empirical means to quantify sampling errors on allele frequencies. No significant differences in allele frequencies and F_{ST} values over all loci were observed between temporal samples of all baseline populations, such that correlation of allelic frequencies between both periods averaged 95% (Tessier & Bernatchez 1999). This allowed us to pool samples from both periods, which resulted in large and similar sample size (average = 78, Rivière-aux-Saumons = 78, Ashuapmushuan = 81, Métabetchouane = 80, Ouasiemsa = 73) for all baseline populations, which also contributes further to reduce biases in assignment (Cornuet *et al.* 1999; Davies *et al.* 1999). Moreover, Lake St-Jean is a closed system offering the important advantage that all possible populations contributing to the mixture are known, eliminating all sources of error coming from others potential populations of origin.

DNA extraction and microsatellite analysis

DNA was extracted from 5–11 noncleaned dried scales conserved in paper envelopes and identified by date and sector for each fish caught (provided by O. Gauthier, Société Faune et Parcs du Québec). Scale digestion was performed overnight at 37 °C in 375 μ L lysis buffer (40 mM Tris-HCl pH 9.0, 50 mM KCl, 0.5% Tween 20), with 10 μ L of proteinase K 20 mg/mL. DNA extraction and concentration were then performed according to Nielsen *et al.* (1997), using 50 μ m microconcentrators (Amicon®). DNA was eluted with distilled water at the end of the second concentration round to a final volume of 50 μ L.

Allelic diversity was resolved at six microsatellite loci. Five of them (*Ssa171* and *Ssa197*, O'Reilly *et al.* 1996; *SSOSL85*, Slettan *et al.* 1995; *MST-3* and *MST-79.1*, Presa & Guyomard 1996) were used previously to assess genetic differentiation among the four populations of the lake (Tessier *et al.* 1997; Tessier & Bernatchez 1999). Locus *Sfo-23* used in those studies was dropped because of its unreliability with old-scale analysis. Instead, we used the locus

Ssa202 developed for *Salmo salar* (O'Reilly *et al.* 1996), which was first analysed to estimate allele frequencies in baseline populations (data available upon request) using the same individuals that were genotyped at the other five loci. Samples were analysed using the fluorescent detection method. For each locus, one of the primers was 5'-labelled with one of three different colours: yellow (HEX) for *Ssa197* and *Ssa202*, green (TET) for *SSOSL85*, *Ssa171* and *MST-79.1*, and blue (FAM) for *MST-3*. Duplex polymerase chain reactions (PCR) were conducted for *Ssa171/Ssa202* and *MST-3/MST-79.1*, whereas *SSOSL85* and *Ssa197* were amplified separately. PCRs were carried out in a 10- μ L reaction volume containing 1 μ L (50–100 ng) of total DNA, 1 μ L of reaction buffer (10 mM Tris-HCl, pH 9.0, 1.5 mM MgCl₂, 0.1% Triton X-100, 50 mM KCl), 2 units of *Taq* DNA polymerase, 75 μ M of each dNTP. Primer concentrations were 0.1 μ M for *MST-3* and 0.2 μ M for *MST-79.1*, 0.5 μ M for *Ssa171* and *Ssa202*, 0.16 μ M for *Ssa197*, and 0.15 μ M for *SSOSL-85*. PCR amplifications were conducted in a Perkin–Elmer 9600 thermocycler (Version 2.01), with the same profile: an initial 2-min denaturing step at 95 °C, followed by 40 cycles of 30 s at 95 °C, 30 s at 56 °C (annealing) and 30 s at 72 °C (elongation). We used, respectively, 1.5 and 1.0 μ L of duplex and simplex PCR products for the polyacrylamide gel migration on automated sequencer (ABI Prism 377). Electrophoresis conditions and allelic size determination followed Garant *et al.* (2000).

Classification methods

The individual population assignment test was first performed according to Paetkau *et al.* (1995), with alleles observed in individuals of unknown origin but absent in baseline populations being added to all populations at a frequency of $1/2N$ (N = number of individuals in a population) (Waser & Strobeck 1998). The level of resolution of the assignment test was determined using both empirical data and simulated genotypes, as detailed by Roques *et al.* (1999). The empirical method consisted of using individuals from baseline populations as if they were of unknown origin, and in assigning them according to the likelihood that their multilocus genotypes occur in each of the baseline population. Each individual to be classified was first removed from its own population for allele frequency estimation of the baseline population (Waser & Strobeck 1998). In the simulation method, 500 multilocus genotypes were generated for each population, by randomly sampling alleles according to their observed frequencies. Individual results were compiled to estimate the relative proportion of fish from each population in a given sample. Each value of proportion estimate for a given sample was taken as the parameter of a binomial distribution, and 95% confidence intervals (CI) around this

value were computed using equations 6.15 and 6.16 in Ostle (1963, p. 94):

$$C(n,x)p^x(1-p)^{n-x} = (1-\gamma)/2 \quad (6.15) = \text{upper limit}$$

$$C(n,x)p^x(1-p)^{n-x} = (1-\gamma)/2 \quad (6.16) = \text{lower limit}$$

where γ is the expected confidence degree (e.g. $\gamma = 0.95$), p the proportion of fish from a given population [number of fish classified in this population (f)/total number of fish in the mixture (n)], and x the variable (upper or lower limit). All assignments were performed using a program written with the algebraic computer system Maple V, version 5, as outlined in Bernatchez & Duchesne (2000).

We also compared the results of this method with those obtained with a classification method based on a prior assessment of probability density of allele frequencies in populations (Rannala & Mountain 1997). The assignment success of this method was assessed using individuals from baseline populations as an unknown mixture file. We also performed the assignment of the unknown mixture of individuals from 1976 ($N = 266$). This analysis was performed using GENECLASS Version 1.0.02 (Cornuet *et al.* 1999) available at <http://www.ensam.inra.fr/URLB/geneclass/geneclass.html>. Overall assignment success obtained with the two methods was almost identical, 89.4 and 88.3%, respectively for the method of Rannala & Mountain (1997) and the Paetkau's assignment test, and estimated proportions from both methods for the 1976 admixture of individuals were almost perfectly correlated ($r = 0.998$, $P = 0.002$). Consequently, only the results from the individual assignment test (Paetkau *et al.* 1995) were used for further analyses.

MSA was conducted with the SPAM program, Version 3.2 (Debevec *et al.* 2000). MSA through SPAM searches for the maximum likelihood estimates of population proportions in a mixture using both conjugate gradient (Pella *et al.* 1996) and expectation-maximization (Pella & Milner 1987) algorithms. The power of the MSA method was assessed using both empirical data and simulations. We first used the baseline data set, composed of approximately equal numbers of fish from each population, and submitted it as a mixture file in order to obtain estimated proportions. Second, simulation was performed to estimate the proportions of each population in a mixture with different contributions. We used the mean estimated proportions from the assignment test for all periods as a value of expected proportions of each population (see values in Table 3, simulated/true contribution). A total of 500 multilocus genotypes was simulated following those proportions and estimated proportions were calculated. Estimations for both methods consisted of the mean of 1000 bootstraps replicates, where both baseline and mixture were resampled, and 95% CI values around estimates

were calculated from the distribution of replicates. We then determined the proportions of the four populations in mixtures of unknown individuals *per se*. Again, both baseline and mixture files were bootstrapped 1000 times and 95% CIs were computed to assess accuracy of estimates.

The congruence between estimates of population relative contribution obtained from both the individual assignment and MSA methods was estimated by computing Pearson's correlation using STATISTICA Version 4.5 (Statistica 1994; Statsoft Inc.).

Spatiotemporal distribution of populations

Because the overall proportions obtained from the individual assignment test and MSA were highly correlated (see Results), statistical analysis of the spatiotemporal distribution was based on the results of the assignment test only. This was performed by statistically comparing proportions by sector, between years within period and among periods by χ^2 randomization tests (Roff & Bentzen 1989) with 1000 permutations using the MONTE program of the REAP software package (McElroy *et al.* 1992). We further assessed the relative importance of spatial and temporal variation in explaining the pattern of variance in the relative proportion of each population observed in each mixed sample for each period by performing a multivariate analysis of variance (MANOVA) using the SAS system Version 6.12 (SAS Institute Inc.). After controlling for multidimensional normality of the data set, F -values associated with the Wilks's lambda statistic were used to test for both null hypotheses of no overall sector or period effects on the relative proportion of each population in each mixed sample. The structure of our data set only allowed us to test for individual effects of temporal and spatial axis on the proportions of each population, whereas assessing the interaction between both effects would have required more degrees of freedom.

The degree of spatial overlap for each population pair was quantified according to Schoener's (1968) formulae of similarity index, $D = 1 - 1/2 \sum |p_i - q_i|$ for $i =$ north, south-east, south-west, central and Desbiens' bay sectors, where p_i and q_i are the estimated proportions of fish from populations p and q in sector i . Proportions were calculated as the number of fish from population p in sector i divided by the total number of fish from population p over all sectors, after the total number of fish sampled in each sector had been standardized for a common sample size. We also considered the possibility that the extent of spatial overlap among populations could be potentially biased by misassignment. As the proportion of misassigned fish may be correlated to the extent of genetic differentiation among baseline populations (see Results), this may also introduce a bias in the estimate of correlation between spatial overlap and genetic differentiation. This problem was corrected as

Table 2 Proportion of individuals from each baseline salmon populations correctly assigned to its origin and misassigned to other populations, based on both the empirical and simulated methods

Method	True origin	Classified in				N	Mean success (%)
		RS	As	Met	Oua		
Empirical method							
	RS	0.94	0.04	0.01	0.01	78	88.3
	As	0.06	0.79	0.01	0.14	81	
	Met	0.03	0.01	0.96	0.00	80	
	Oua	0.05	0.11	0.0	0.84	73	
Simulation method							
	RS	0.97	0.02	0.01	0.00	500	94.3
	As	0.03	0.88	0.01	0.08	500	
	Met	0.01	0.00	0.99	0.00	500	
	Oua	0.01	0.06	0.00	0.93	500	

RS: Rivière-aux-Saumons, As: Ashuapmushuan, Met: Métabetchouane, Oua: Ouasiemsca populations. *N* represents the total sample size for each population in the empirical method and the number of simulated individuals in the simulation method.

follows. Table 2 provides the most likely proportions of misassignment from one population to the others (see also Results). One can then assume that the number of fish assigned to each population is the sum of individuals correctly assigned to its origin plus those from the other populations that were misassigned to it. We can thus compute the most likely number of fish really belonging to the four populations that would result in the observed assignment numbers, given the probable misassignment proportions. This can be achieved by solving a system of five equations with four unknown parameters (x, y, z, w), which correspond to the four numbers we seek to quantify. For instance, 93 salmon were assigned to the As population in the north sector in the 1970s. We thus have $93 = 0.88x + 0.02y + 0.00z + 0.06w$, where 0.88 is the proportion of fish correctly assigned to the As population, 0.02 is the likely proportion of RS fish wrongly assigned to the As population, etc. Misassignment proportions obtained from the simulation method were used because possible solutions to the equation system could not be obtained for several sectors when using those derived from the empirical method.

We then compared the spatial overlap index with the extent of genetic differentiation obtained from microsatellites and MHC markers using Mantel's test and Pearson's correlation coefficient. Values of F_{ST} obtained from Tessier & Bernatchez (1999) were averaged over time for microsatellites and estimates for MHC were from Landry & Bernatchez (2001). MHC data consisted of allelic variation screened at the MHC class II B locus using single-strand conformation polymorphism analysis (SSCP). The reliability of the SSCP gel scoring was confirmed by sequencing analysis of identified SSCP alleles (detailed in Landry & Bernatchez 2001). Finally, we evaluated the Pearson's correlation coefficient between the extent of spatial overlap

of populations pairs and the geographical distance between their respective river outlets.

Results

Congruence between individual assignment test and mixed-stock analysis

Both the individual assignment test and MSA were efficient for estimating the relative contribution of the four salmon populations to samples of unknown origin. For the assignment test, the mean classification success for the simulated method was 94.3% (Table 2). Estimates obtained from the empirical method were lower but still high, with an overall assignment success of 88.3% (Table 2). For both methods, misassignment of individuals of a given population to one of the other three populations was consistent with the extent of genetic divergence among populations reported in Tessier & Bernatchez (1999). For example, the lowest misassignment values were observed for the Métabetchouane population, this river being the most genetically distinct. Highest misclassifications values were observed between the Ashuapmushuan and Ouasiemsca populations, which are the most similar genetically. For MSA, contribution estimates were very accurate (Table 3), being within 0.39 and 2.52% of the true contribution for the baseline and simulated data, respectively. The estimates were also precise, with a maximum standard deviation (SD) of 3.26 and 3.13% and maximum CI width of 12.99 and 11.17% for the baseline and simulated data, respectively.

Estimates of the overall proportions of the four populations for each temporal period or particular samples (central and Desbiens' Bay sectors) obtained from the MSA and the individual assignment test were also highly

Data set	Populations	Mixed-stock analysis				
		True contribution (%)	Mean estimate (%)	SD	95% CI	
					Lower	Upper
Baseline	RS	24.8	24.9	3.0	19.2	31.1
	As	26.1	25.7	3.3	19.4	32.4
	Met	25.7	25.6	2.9	20.0	31.5
	Oua	23.5	23.9	3.0	18.1	29.5
Simulated	RS	16.0	15.6	1.9	11.6	18.8
	As	47.0	44.5	3.1	39.4	50.5
	Met	8.0	7.2	1.1	4.9	9.8
	Oua	29.0	28.6	3.0	22.4	33.5

RS: Rivière-aux-Saumons, As: Ashuapmushuan, Met: Métabetchouane, Oua: Ouasiemscas populations.

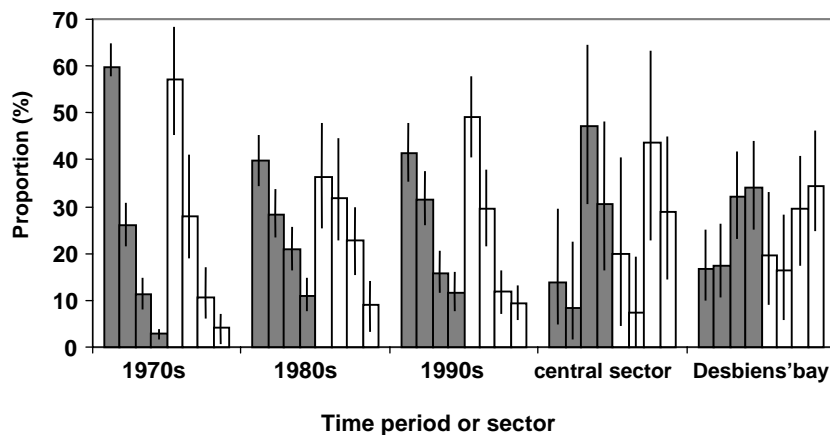


Table 3 Efficiency of mixed-stock analysis to estimate contributions of each population for a mixture composed of the baseline populations and simulated genotypes

Fig. 2 Comparison of the proportions of the four populations estimated from the individual assignment method (grey bars) and mixed-stock analysis (white bars) for the different periods and sectors. In order for each comparison: Ashuapmushuan, Ouasiemscas, Rivière-aux-Saumons, Métabetchouane. Vertical bars represent 95% confidence intervals on estimates.

correlated ($r^2 = 0.95$ and $P < 0.000001$). Differences between estimates of the two methods were always $< 4\%$, with two exceptions (Fig. 2). The two largest discrepancies were observed for the 1990s and the central sector, where differences of 7.85 and 5.87% were observed for the Ashuapmushuan contribution estimates, respectively. For the three periods, CIs around the individual assignment were generally smaller than those obtained for the MSA, their mean width being 8.6 and 15.3%, respectively. Given this, and the generally high congruence observed between both methods, the detailed analysis of spatiotemporal distribution of the different populations was pursued with the individual assignment test only.

Temporal stability of overall proportions

Within each of the three periods, no significant difference was observed in the overall proportions of the different populations between consecutive years (Table 4). Fish from consecutive years were consequently pooled to

Table 4 Statistical comparison of the observed proportions of populations among consecutive years for each period

Period	Year	N	Proportions (%)				χ^2	P-value
			RS	As	Met	Oua		
1970s	1975	92	17.4	53.3	5.4	23.9	7.62	0.06 \pm 0.007
	1976	266	9.0	62.0	2.3	26.7		
1980s	1986	241	22.1	39.4	12.4	26.1	4.08	0.24 \pm 0.01
	1987	86	17.4	40.7	7.0	34.8		
1990s	1994	54	9.3	46.3	20.4	18.0	8.15	0.24 \pm 0.01
	1995	76	18.4	43.4	9.2	28.9		
	1996	133	16.4	38.4	9.1	36.1		

RS: Rivière-aux-Saumons, As: Ashuapmushuan, Met: Métabetchouane, Oua: Ouasiemscas populations.

compare proportions among the three periods. Fish from the central sector caught in 1999 and 2000 were also pooled as no significant difference of proportions was observed between years ($\chi^2 = 1.14$ and $P = 0.812$). When considered

regardless of spatial distribution, overall proportions showed that the four populations were not represented equally in the samples analysed from the recreational fishery. Confidence intervals were generally nonoverlapping, with the exception of Rivière-aux-Saumons/Ouasiemscas for the 1980s, and Rivière-aux-Saumons/Métabetchouane and Ashuapmushuan/Ouasiemscas for the 1990s (Fig. 2). The hierarchy in proportions followed the same trend for all periods: Ashuapmushuan > Ouasiemscas > Rivière-aux-Saumons > Métabetchouane populations (Fig. 2). However, the estimated proportions of each population varied significantly among periods ($\chi^2 = 47.22$ and $P < 0.0001$), which therefore rejected the null hypothesis of temporal stability in relative representation of each population. This was entirely due to the highly significant differences between the 1970s and the two other periods (1970s to 1980s: $\chi^2 = 39.75$ and $P < 0.0001$; 1970s to 1990s $\chi^2 = 29.68$ and $P < 0.0001$). Namely, the Ashuapmushuan contribution decreased significantly from 59.9 to 39.8% between the 1970s and 1980s, whereas that of Rivière-aux-Saumons and Métabetchouane increased from 11.2 to 20.8%, and 3.0 to 11.0%, respectively (Fig. 2). No significant differences were observed between the 1980s and the 1990s ($\chi^2 = 2.74$ and $P = 0.443$), and these two periods were pooled for the analysis of spatial distribution.

Heterogeneity in spatial distribution among populations

A differential pattern of spatial distribution was observed among the four populations for both periods (Table 5). For both periods, this was due to differences between the north sector and the other two (Fig. 3). Thus, the Ashuapmushuan population predominated in relative abundance in the north sector, reaching 75.8% in the 1970s, whereas both the Métabetchouane and Rivière-aux-Saumons populations were under-represented relative to

Table 5 Statistical comparison of proportions of the four populations among sectors for each period

Period	Comparison	χ^2	<i>P</i> -value
1970s	TOTAL	26.46	< 0.0001
	N vs. SE	20.32	< 0.0001
	N vs. SW	21.72	< 0.0001
	SE vs. SW	1.24	0.787 ns
1980/1990s	TOTAL	62.60	< 0.0001
	N vs. SE	47.44	< 0.0001
	N vs. SW	41.98	< 0.0001
	SE vs. SW	8.09	0.045 ns

TOTAL refers to comparisons among the three sectors, N: north, SE: south-east and SW: south-west. ns: nonsignificant following sequential Bonferroni correction for multiple tests.

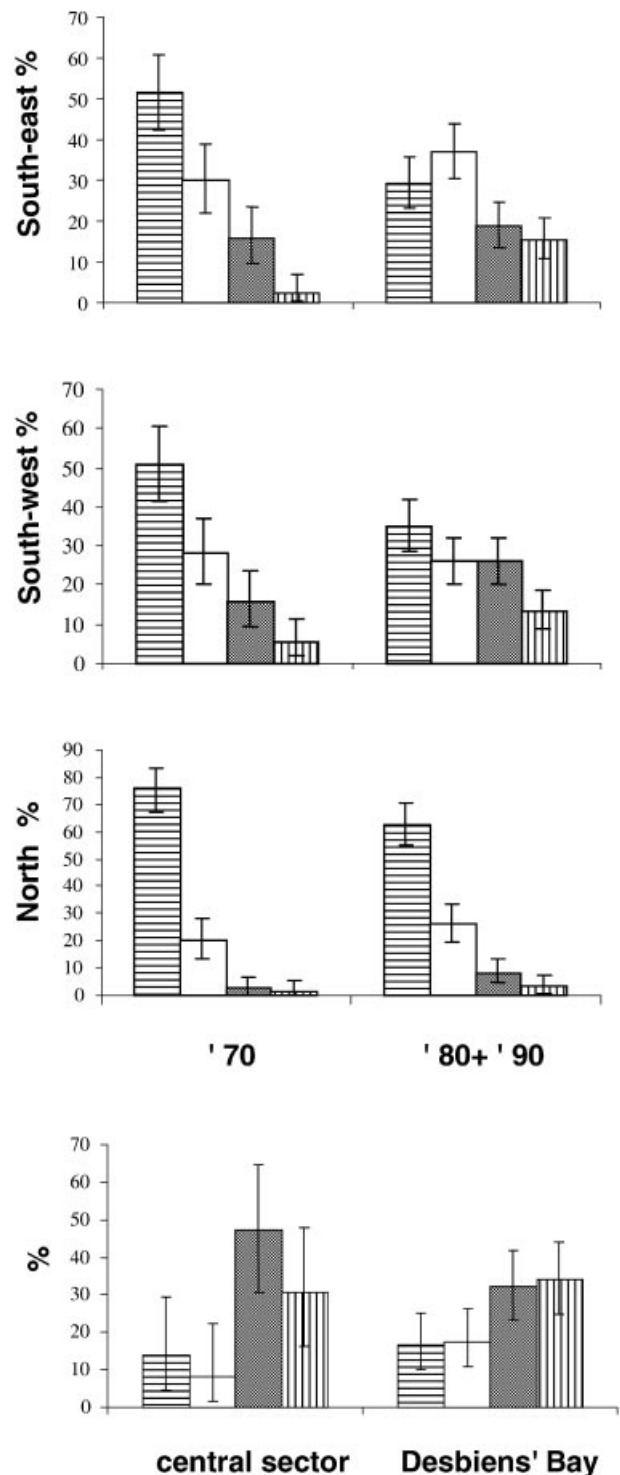


Fig. 3 Estimated proportions (in %) of each population for the different sectors and temporal periods. Sample sizes were 124 (N, 1970), 161 (N, 1980/1990), 120 (SE, 1970), 209 (SE, 1980/1990), 114 (SW, 1970), 220 (SW, 1980/1990), 103 (Desbiens' Bay) and 49 (Central Sector). Vertical bars are the 95% confidence intervals on proportion estimates. Populations symbols are Ashuapmushuan: horizontal lines, Ouasiemscas: white, Rivière-aux-Saumons: dark grey and Métabetchouane: vertical lines.

their proportions in the other two sectors. Namely, salmon from the Métabetchouane were almost absent in the north sector, with proportions varying from 1.6 to 3.1%. The relative proportion of all four populations in the north sector was stable temporally as no significant differences in the proportions of the four populations was observed between periods ($\chi^2 = 8.83$ and $P = 0.201$). Globally, the relative proportions in the other two sectors contrasted less sharply (Table 5, Fig. 3). In fact, the null hypothesis of similar proportions for the two sectors was not rejected for the 1970s, whereas only marginal differences were observed for the 1980s to 1990s. In both sectors, the Ashuapmushuan population was still the most represented, except for the south-east sector where an increased proportion of the Ouasiemsca population was observed for the 1980s to 1990s. A more even distribution of proportion of the four populations was observed for that period, particularly for the south-west sector, as shown by the more pronounced overlap in CIs.

Although the various individual statistical tests on proportions revealed significant differences in both time and space, results of the MANOVA showed that overall, the variance observed in the spatial distribution of the different populations was more pronounced than that observed in time. Thus, this analysis rejected the null hypothesis of no overall spatial effect ($F = 6.2362$, $P = 0.049$, $df = 6$), whereas the null hypothesis of no overall temporal effect could not be rejected ($F = 1.97$, $P = 0.2665$, $df = 6$). This indicates that the significant differences observed in the relative proportions of the four populations in different sectors of the lake have remained relatively stable over 25 years.

The differential pattern of spatial distribution among populations was further supported by the contrasting results observed for the central and Desbiens' Bay sectors compared with the others. Namely, the central sector sampled in the 1990s differed significantly from the other three sectors sampled during this period ($P < 0.002$ in all three comparisons). There was a strong trend for both Rivière-aux-Saumons and Métabetchouane populations to be over-represented in this sector, whereas they were the least abundant elsewhere. In fact, the confidence interval of the Métabetchouane population did not overlap with that of either the Ashuapmushuan or Ouasiemsca populations. A similar trend of differential abundance of each population was observed for the Desbiens' Bay sector, where proportions differed significantly ($P < 0.0001$) from those observed in the three other sectors sampled for the same period (1970s). In contrast, proportions observed in the Desbiens' Bay did not differ significantly from those of the central sector ($\chi^2 = 3.40$ and $P = 0.331$). Thus, results for Desbiens' Bay and central sectors closely matched, whereas they differed from those obtained in the other three sectors.

The overall trend in differential distribution between the two population groups (Ashuapmushuan/Ouasiemsca vs. Rivière-aux-Saumons and Métabetchouane) was further illustrated by the extent of spatial overlap. Thus, although the overall value of the index was relatively high (mean $D = 0.59$), the two most pronounced measures of overlap were observed between the Ashuapmushuan and Ouasiemsca ($D = 0.78$), and the Rivière-aux-Saumons and Métabetchouane ($D = 0.74$) populations. In comparison, the spatial overlap between Ashuapmushuan and Rivière-aux-Saumons was much lower ($D = 0.51$). The lowest extent of overlap was observed between the Métabetchouane and both the Ashuapmushuan ($D = 0.35$) and the Ouasiemsca ($D = 0.48$) populations, whereas overlap between Rivière-aux-Saumons and Ouasiemsca was intermediate ($D = 0.65$).

A strong and statistically significant negative correlation was observed between the F_{ST} calculated from MHC and the spatial overlap index ($r = -0.93$, $P = 0.007$) (Fig. 4). A strong correlation, although not significantly different from zero, was also observed for microsatellites ($r = -0.74$, $P = 0.09$). A closer examination of Fig. 4 revealed that the latter lack of significance was most likely explained by the outlying Métabetchouane/Rivière-aux-Saumons value. Indeed, F_{ST} values calculated from microsatellites

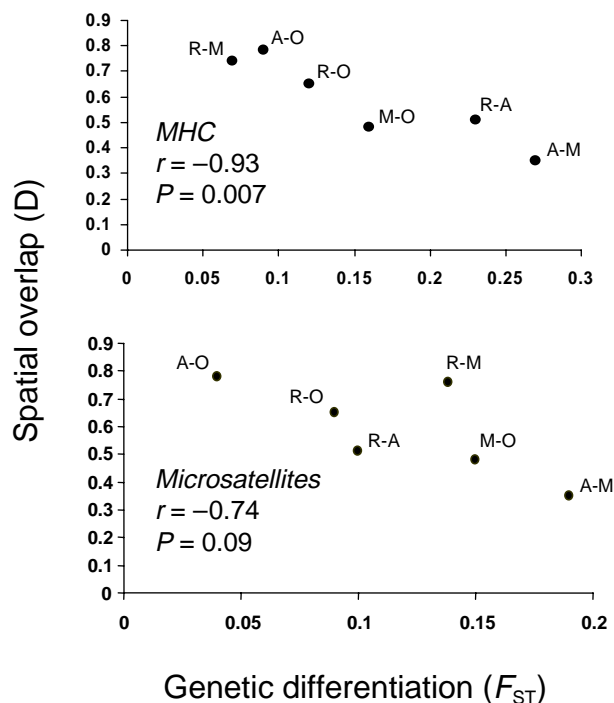


Fig. 4 Relationship between spatial index overlap and the extent of genetic differentiation (F_{ST}) among populations, estimated from MHC class II B locus and microsatellites. A: Ashuapmushuan, O: Ouasiemsca, R: Rivière-aux-Saumons, M: Métabetchouane.

and overlap index were strongly negatively correlated when omitting this value ($r = -0.96$, $P = 0.009$). In contrast, no significant correlation was found between the extent of spatial overlap for each population pair and the geographical distance between their river outlets ($r = 0.01$, $P = 0.85$).

Discussion

Horizontal segregation of sympatric salmon populations

The first objective of this study was to test the null hypothesis of homogeneity in the horizontal distribution of the proportion of four sympatric salmon populations in Lake St-Jean. This was refuted, as the relative proportions of the four populations varied among lake sectors for each period. Despite the fact that the overall proportion of each population varied over time, several features of the pattern of differential distribution remained temporally stable. Most noticeable was an apparent dichotomy of distribution between the two population groups formed by the Ashuapmushuan/Ouasiemsca, and the Rivière-aux-Saumons/Métabetchouane populations, respectively. The first two populations were ubiquitous in their distribution throughout the three coastal sectors, with the exception that the Ouasiemsca population tended to avoid the north relative to the other two sectors. Thus, the north sector was the area of the lake where the Ashuapmushuan population was the most prevalent at all times. In contrast, both the Métabetchouane and Rivière-aux-Saumons populations were clearly under-represented in the north sector at all times, whereas they dominated in relative abundance in the centre and Desbiens' Bay sectors. Consequently, our results indicated that sympatric salmon populations differentially occupied the various sectors of the lake in a somewhat predictive manner over the last 25 years.

Before concluding that this pattern does indeed provide evidence of biologically meaningful spatial niche partitioning, alternative explanations must be considered. An obvious explanation would be that the different populations are distributed differentially due to limited lacustrine movement and according to geographical proximity of their river of origin. This, however, appears unlikely as a geographical distance of 40 km (the maximum diameter of the lake) is most likely a minor constraint for salmon. Furthermore, there was no significant correlation between the distance from the outlet of the river of origin to the middle point of a given sector and proportions of the four populations in each sector, for either the 1970s ($r = 0.1744$ and $P = 0.588$) or the 1980s/1990s ($r = 0.1227$ and $P = 0.704$). A case in point is the Ouasiemsca population which was always less represented in the north sector (the closest to this river outlet) and reached its higher proportion in the

sector farthest (south-east) from its river of origin. More striking was the fact that salmon from the Rivière-aux-Saumons, a tributary of the Ashuapmushuan, showed a very contrasting pattern of distribution relative to the latter population, reaching its lowest contribution in the north sector where Ashuapmushuan dominated numerically.

A second point to consider is that the observed pattern of spatial heterogeneity has no biological meaning as related to niche partitioning, as spatial overlap values were relatively high on average. We cannot refute this possibility, however, comparisons with other studies suggest that at least the lowest values of overlap may be biologically meaningful. Several studies using Schoener's similarity index to estimate diet overlap between fish considered a threshold of ≈ 0.60 as being of biological significance (Sandlund *et al.* 1987; Scrimgeour & Winterbourn 1987; Naesje *et al.* 1991; Lucena *et al.* 2000). In this study, the hypothesis of biologically significant differences in spatial overlap index was further supported by the fact that population partitioning among lake sectors remained rather constant over a period of 25 years. Moreover, it is possible that the extent of spatial segregation was underestimated due to the fact that sectors were determined a priori on geographical, rather than biological, criteria for fisheries management purposes.

Spatial partitioning on the horizontal axis does not exclude the contribution of additional factors to salmon niche partitioning in Lake St-Jean. For instance, although rainbow smelt compose the major part of the diet for salmon in the lake, it is possible that alternative and less important prey are used differentially by salmon of different populations. Namely, a study of stomach content performed from 1997 to 1999 showed lower proportions of rainbow smelt in the stomachs of fish in the north sector relative to proportions for fish caught in the south-east and south-west sectors (M. Legault, unpublished data). It is also possible that salmon populations prey differentially upon different smelt populations. Indeed, an ongoing study provided evidence for the occurrence of genetically distinct dwarf and normal smelt populations in the lake (R. Saint-Laurent, unpublished data). This could make possible a prey-predator association between salmon and smelt populations.

Further support for the biological significance of differential distribution was provided by the negative correlation between spatial overlap and the extent of genetic differentiation observed at both MHC and microsatellites. Again, the main case in point was the pronounced levels of both genetic (particularly at MHC) and spatial differentiation between Rivière-aux-Saumons and Ashuapmushuan. In contrast, Ashuapmushuan was more similar, genetically and in distribution, to the Ouasiemsca population which reproduces in a distinct river drainage. In summary, and despite the fact that the negative correlation between

genetic differentiation and spatial overlap did not differ statistically from zero when including all comparisons for microsatellites, these observations are clearly more supportive of an association between the extent of genetic differentiation and that of spatial niche partitioning than the absence of it. If true, what determines such a correlation? One possible determinant of such a correlation is that the variable extent of genetic and spatial differentiation could be a consequence of directional selective pressures promoting population-specific specializations for sharing ecological niches in sympatry (Bernatchez *et al.* 1999). Such selective pressures are associated with the fitness cost of producing hybrids of intermediate phenotypes, which are predicted to increase with the extent of niche partitioning reached between parental populations (Schluter 1998; Hatfield & Schluter 1999). The extent of reproductive isolation between populations is expected to evolve accordingly and, consequently, one would predict that genetic differentiation should be more pronounced between populations that are more differentiated in their ecological niches (Bernatchez *et al.* 1999). In the case of salmon populations that do not exhibit obvious morphological specialization, ecological niche partitioning could be achieved by differential behaviour for spatial use. Many studies have provided evidence of a heritable basis for behavioural differences in fish, as well as their adaptive significance (Raleigh 1967, 1971; Kelso *et al.* 1981; Riddell & Leggett 1981; Nordeng 1983; Taylor & Foote 1991; Northcote 1992; Skúlason *et al.* 1993). For the salmon of Lake St-Jean, adaptive differences could be in the form of genetically based behavioural differences for foraging in different areas of the lake. Thus, the more differentiated salmon from different populations are in spatial niche partitioning, the higher the fitness cost of intermediate hybrids would be, and more pronounced reproductive isolation mechanisms would evolve between them. This would not exclude the possibility that some populations may be more generalist (e.g. Ashuapmushuan.) than others (e.g. Métabetchouane) in spatial use.

Analysis of population admixture from an individual-based approach

Overall, the use of allele frequency-based individual assignment proved reliable in estimating admixture proportions of different salmon populations in Lake St-Jean. It is, however, important to note that interpreting high assignment success as an indication of methodological reliability implicitly assumes limited sampling errors in the estimates of allele frequencies in baseline populations. Clearly, increased sampling errors may result in reduced exactitude and precision of assignment (Cornuet *et al.* 1999). Although the exact effect of sampling errors cannot be easily accounted for, the characteristics of our baseline populations (high sample

size, temporal stability of allelic frequencies, HWE, all source populations sampled) strongly suggest that it was not a significant problem in this study.

Admittedly, and as in most studies to date (but see Roques *et al.* 1999; Olsen *et al.* 2000), we used the least stringent selection criterion of assignment of log likelihood ratio (LLR) = 0. Under this criterion, individuals were assigned to a given population simply on the basis of the highest likelihood of occurrence. That is, all individuals were classified at the possible cost of increased misassignment. Using more stringent selection criteria would reduce the probability of misassignment, but also the total number of assigned individuals (e.g. Roques *et al.* 1999). In our study, assignment success of fish from baseline populations decreased to 69, 62 and 40% for LLR values of 1, 1.3 and 2, respectively. Although this may seem more desirable at first, there were two potential problems in increasing the stringency of the selection criterion in this study. First, the reduction in the total number of assigned fish would have lowered our efficiency (i.e. increase variance on estimates) in quantifying the relative proportions of populations in different sectors. More importantly, the proportion of nonassigned fish would not have been distributed evenly among all populations, being concentrated mainly on populations with the lowest assignment success, that is the Ashuapmushuan the Ouasiemscas populations. This would have caused important biases of proportion estimates. For example, for LLR = 2, the proportion of nonassigned fish would have been four times more important for the Ashuapmushuan population than for the Métabetchouane. We therefore chose to use a low selection criterion and compared estimates of relative proportion based on individual multilocus genotype identification with those obtained by the more widely applied MSA. Estimates of admixture proportion based this method were both exact and precise. More importantly, estimates obtained using both MSA and individual multilocus genotype methods were highly congruent and almost perfectly correlated, despite their different analytical approaches. This implies that both methods may have similar outcomes when estimating admixture proportions, although their relative usefulness may vary in specific contexts, for instance, when it is necessary to obtain information of specific individuals for conservation purposes (e.g. Olsen *et al.* 2000). In contrast, estimates of admixture proportions based on MSA may still be reliable when only low polymorphic markers are available (e.g. Pigeon *et al.* 1998; Scribner *et al.* 1998), whereas the use of individual assignment may be very limited in such cases (Estoup *et al.* 1998; Olsen *et al.* 2000). Both the frequency-based method of individual assignment (*sensu* Paetkau *et al.* 1995) and the MSA were particularly efficient in this study because reliable a priori knowledge of allele frequencies was available for all possible baseline populations. When this is not the case, alternative methods

should be considered. In general, the method of Rannala & Mountain (1997) is theoretically more suited to coping with deviations from the true allele frequencies in populations, although the evaluation of its performance via either computer simulation or empirical investigations conducted to date indicated that the efficiency of this approach may only be slightly better than the frequency method in most circumstances (Cornuet *et al.* 1999; Primmer *et al.* 2000; this study). More important is the need to estimate the statistical confidence of each individual assignment when allele frequency data are not available from all possible populations of origins (Cornuet *et al.* 1999).

In summary, this study provides evidence for differential patterns in the horizontal distribution among sympatric lacustrine fish populations, resulting in their spatial niche partitioning. The temporal stability of this pattern, the lack of an association between the spatial partitioning and the geographical distance between rivers of origin, and the possible negative correlation between spatial overlap and genetic differentiation support the hypothesis that this pattern reflects the outcome of selective pressures driving behavioural differences for spatial niche partitioning among populations. Comparative analysis of fish admixture showed that individual assignment and MSA performed equally well, although their suitability may differ in specific contexts.

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References

Beacham TD, Gould AP, Withler RE, Murray CB, Barner LW (1987) Biochemical genetic survey and stock identification of chum salmon (*Oncorhynchus keta*) in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, **44**, 1702–1713.

Beacham TD, Wood CC (1999) Application of microsatellite DNA variation to estimation of stock composition and escapement of Nass River sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 297–310.

Bernatchez L, Chouinard A, Lu G (1999) Integrating molecular genetics and ecology in studies of adaptive radiation: whitefish, *Coregonus* sp., as a case study. *Biological Journal of the Linnean Society*, **68**, 173–194.

Bernatchez L, Duchesne P (2000) Individual-based genotype analysis in studies of parentage and population assignment: how many loci, how many alleles? *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 1–12.

Cornuet J-M, Piry S, Luikart G, Estoup A, Solignac M (1999) New methods employing multilocus genotypes to select or exclude populations as origin of individuals. *Genetics*, **153**, 1989–2000.

Davies N, Villablanca FX, Roderick GK (1999) Determining the source of individuals: multilocus genotyping in nonequilibrium population genetics. *Trends in Ecology and Evolution*, **14**, 17–21.

Debevec EM, Gates RB, Masuda M, Pella J, Reynolds J, Seeb LW (2000) SPAM (Version 3.2): statistics program for analyzing mixtures. *Journal of Heredity*, **91**, 509–510.

Estoup A, Angers B (1998) Microsatellite and minisatellites for molecular ecology: theoretical and experimental considerations. In: *Advances in Molecular Ecology* (ed. Carvalho G), pp. 55–86. IOS Press, Amsterdam, The Netherlands.

Estoup A, Rousset F, Michalakis Y *et al.* (1998) Comparative analysis of microsatellite and allozyme markers: a case study investigating microgeographic differentiation in brown trout (*Salmo trutta*). *Molecular Ecology*, **7**, 339–353.

Fournier DA, Beacham TD, Riddell BE, Busack CA (1984) Estimating stock composition in mixed stock fisheries using morphometric, meristic, and electrophoretic characteristics. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 400–408.

Garant D, Dodson JJ, Bernatchez L (2000) Ecological determinants and temporal stability of the within-river population structure in Atlantic salmon (*Salmo salar* L.). *Molecular Ecology*, **9**, 615–628.

Gíslason D, Ferguson MM, Skúlason S, Snorrason SS (1999) Rapid and coupled phenotypic and genetic divergence in Icelandic Arctic Char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 2229–2234.

Hatfield T, Schluter D (1999) Ecological speciation in sticklebacks: environment-dependent hybrid fitness. *Evolution*, **53**, 866–873.

Kelso BW, Northcote TG, Wehrhahn CF (1981) Genetic and environmental aspects of the response to water current by rainbow trout (*Salmo gairdneri*) originating from inlet and outlet streams of two lakes. *Canadian Journal of Zoology*, **59**, 2177–2185.

Landry C, Bernatchez L (2001) Comparative analysis of population structure across environments and geographical scales at major histocompatibility complex and microsatellite loci in Atlantic salmon (*Salmo salar*). *Molecular Ecology*, **10**, 2525–2539.

Lu G, Bernatchez L (1999) Correlated trophic specialization and genetic divergence in sympatric lake whitefish ecotypes (*Coregonus clupeaformis*): support for the ecological speciation hypothesis. *Evolution*, **53**, 1491–1505.

Lucena FM, Vaske T, Ellis JR, O'Brien CM (2000) Seasonal variation in the diets of bluefish, *Pomatomus saltatrix* (Pomatomidae) and striped weakfish, *Cynoscion guatucupa* (Sciaenidae) in southern Brazil: implications of food partitioning. *Environmental Biology of Fishes*, **57**, 423–434.

McElroy D, Moran P, Bermingham E, Kornfield I (1992) REAP: an integrated environment for the manipulation and phylogenetic analysis of restriction data. *Journal of Heredity*, **83**, 157–158.

Nadon L (1991) *Évaluation du régime alimentaire et de la croissance de la ouananiche (Salmo salar L.) du lac St-Jean*. MSc Thesis, Université du Québec à Chicoutimi.

Naesje TF, Jonsson B, Sandlund OT, Kjellberg G (1991) Habitat switch and niche overlap in coregonid fishes: effects of zooplankton abundance. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 2307–2315.

- Nielsen EE, Hansen MM, Loeschcke V (1997) Analysis of microsatellite DNA from old scale samples of Atlantic salmon *Salmo salar*: a comparison of genetic composition over 60 years. *Molecular Ecology*, **6**, 487–492.
- Nielsen EE, Hansen MM, Loeschcke V (1999a) Analysis of DNA from old scale samples: technical aspects, applications and perspectives for conservation. *Hereditas*, **130**, 265–276.
- Nielsen EE, Hansen MM, Loeschcke V (1999b) Genetic variation in time and space: microsatellite analysis of extinct and extant populations of Atlantic salmon. *Evolution*, **53**, 261–268.
- Nordeng H (1983) Solution to the 'charr' problem based on Arctic charr (*Salvelinus alpinus*) in Norway. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 1372–1387.
- Northcote TG (1992) Migration and residency in stream salmonids – some ecological considerations and evolutionary consequences. *Nordic Journal of Freshwater Research*, **67**, 5–17.
- O'Reilly PT, Hamilton LC, McConnell SK, Wright JM (1996) Rapid analysis of genetic variation in Atlantic salmon (*Salmo salar*) by PCR multiplexing of dinucleotide and tetranucleotide microsatellites. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 2292–2298.
- Olsen JB, Bentzen P, Banks MA, Shaklee JB, Young S (2000) Microsatellites reveal population identity of individual pink salmon to allow supportive breeding of a population at risk of extinction. *Transactions of the American Fisheries Society*, **129**, 232–242.
- Ostle B (1963) *Statistics in Research: Basic Concepts and Techniques for Research Workers*, 2nd edn. Iowa University Press, Ames.
- Palsbøll PJ, Allen J, Bérubé M *et al.* (1997) Genetic tagging of humpback whales. *Nature*, **388**, 767–769.
- Paetkau D, Calvert W, Stirling I, Strobeck C (1995) Microsatellites analysis of population structure in Canadian polar bears. *Molecular Ecology*, **4**, 347–354.
- Pella JJ, Masuda M, Nelson S (1996) Search algorithms for computing stock composition of a mixture from traits of individuals by maximum likelihood. NOAA Technical Memorandum NMFS-AFSC-61.
- Pella JJ, Milner GB (1987) Use of genetic marks in stock composition analysis. In: *Population Genetics and Fishery Management* (eds Ryman N, Utter F), pp. 247–276. University of Washington Press, Washington, DC.
- Pigeon D, Dodson JJ, Bernatchez L (1998) A mtDNA analysis of spatiotemporal distribution of two sympatric larval populations of rainbow smelt (*Osmerus mordax*) in the St. Lawrence River estuary, Quebec, Canada microsatellites. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1739–1747.
- Presca P, Guyomard R (1996) Conservation of microsatellites in three species of salmonids. *Journal of Fish Biology*, **49**, 1326–1329.
- Primmer CR, Koskinen MT, Piironen J (2000) The one that did not get away: individual assignment using microsatellite data detects a case of fishing competition fraud. *Proceedings of the Royal Society of London, Series B*, **267**, 1699–1704.
- Raleigh RF (1967) Genetic control in the lakeward migration of sockeye salmon (*Oncorhynchus nerka*) fry. *Journal of the Fisheries Research Board of Canada*, **24**, 2613–2622.
- Raleigh RF (1971) Innate control of migrations of salmon and trout fry from natal gravels to rearing areas. *Ecology*, **52**, 291–297.
- Rannala B, Mountain JL (1997) Detecting immigration by using multilocus genotypes. *Proceedings of the National Academy of Sciences of the USA*, **94**, 9197–9201.
- Riddell BE, Leggett WC (1981) Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 308–320.
- Robinson WB, Schluter D (2000) Natural selection and the evolution of adaptive genetic variation in northern freshwater fishes. In: *Adaptive Genetic Variation in the Wild* (eds Mousseau TA, Sinervo B, Endler J), pp. 65–94. Oxford University Press, New York.
- Roff DA, Bentzen P (1989) The statistical analysis of mitochondrial DNA polymorphism: chi-square and the problem of small samples. *Molecular Biology and Evolution*, **6**, 539–545.
- Roques S, Duchesne P, Bernatchez L (1999) Potential of microsatellites for individual assignment: the North Atlantic redfish (genus *Sebastes*) species complex as a case study. *Molecular Ecology*, **8**, 1703–1717.
- Sandlund OT, Naesje TF, Kjellberg G (1987) The size selection of *Bosmina longispina* and *Daphnia galeata* by co-occurring cisco (*Coregonus albula*), whitefish (*C. lavaretus*) and smelt (*Osmerus eperlanus*). *Archiv für Hydrobiologia*, **110**, 357–363.
- Schluter D (1998) Ecological causes of speciation. In: *Endless Forms: Species and Speciation* (eds Howard DJ, Berlocher SH), pp. 114–129. Oxford University Press, New York.
- Schluter D, McPhail JD (1993) Character displacement and replicate adaptive radiation. *Trends in Ecology and Evolution*, **8**, 197–200.
- Schoener TW (1968) The anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology*, **49**, 704–726.
- Scribner KT, Crane PA, Spearman WJ, Seeb LW (1998) DNA and allozyme markers provide concordant estimates of population differentiation: analyses of U.S. and Canadian populations of Yukon River fall-run chum salmon (*Oncorhynchus keta*). *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1748–1758.
- Scrimgeour GJ, Winterbourn MJ (1987) Diet, food resource partitioning and feeding periodicity of two riffle-dwelling fish species in a New Zealand river. *Journal of Fish Biology*, **31**, 309–324.
- Seeb LW, Crane P (1999) Allozyme and mitochondrial DNA discriminate Asian and North American populations of chum salmon in mixed-stock fisheries along the south coast of the Alaska peninsula. *Transactions of the American Fisheries Society*, **128**, 88–103.
- Shaklee JB, Beacham TD, Seeb L, White BA (1999) Managing fisheries using genetic data: case studies from four species of Pacific salmon. *Fisheries Research*, **42**, 45–78.
- Skúlason S, Smith TB (1995) Resource polymorphisms in vertebrates. *Trends in Ecology and Evolution*, **10**, 366–370.
- Skúlason S, Snorrason SS, Ota D, Noakes DLG (1993) Genetically based differences in foraging behaviour among sympatric morphs of arctic charr (*Salvelinus alpinus*). *Animal Behaviour*, **45**, 1179–1192.
- Slettan A, Olsaker I, Lie O (1995) Atlantic salmon, *Salmo salar*, microsatellites at the SSOSL25, SSOSL85, SSOSL311, SSOSL417 loci. *Animal Genetics*, **26**, 281–282.
- Statistica (1994) *Statistica for Windows. General Conventions and Statistics*. StatSoft Inc., Tulsa, OK.
- Taylor EB (1999) Species pairs of north temperate freshwater fishes: taxonomy, evolution, and conservation. *Reviews in Fish Biology and Fisheries*, **9**, 299–324.
- Taylor EB, Foote CJ (1991) Critical swimming velocities of juveniles sockeye salmon and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka* (Walbaum). *Journal of Fish Biology*, **38**, 407–419.
- Taylor EB, Harvey S, Pollard S, Volpe J (1997) Postglacial genetic differentiation of reproductive ecotypes of kokanee *Oncorhynchus nerka* in Okanagan Lake, British Columbia. *Molecular Ecology*, **6**, 503–517.

- Tessier N, Bernatchez L (1999) Stability of population structure and genetic diversity across generations assessed by microsatellites among sympatric populations of landlocked Atlantic salmon (*Salmo salar* L.). *Molecular Ecology*, **8**, 169–179.
- Tessier N, Bernatchez L (2000) A genetic assessment of single versus double origin of landlocked Atlantic salmon (*Salmo salar*) from Lake Saint-Jean, Québec, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 797–804.
- Tessier N, Bernatchez L, Wright JM (1997) Population structure and impact of supportive breeding inferred from mitochondrial and microsatellite DNA analyses in land-locked Atlantic salmon *Salmo salar* L. *Molecular Ecology*, **6**, 735–750.
- Turgeon J, Estoup A, Bernatchez L (1999) Species flock in the North American Great Lakes: molecular ecology of lake *Nipigon ciscoes* (Teleostei: coregonidae: *coregonus*). *Evolution*, **53**, 1857–1871.
- Utter F, Ryman N (1993) Genetic markers and mixed stock fisheries. *Fisheries*, **18**, 11–21.
- Waples RS (1998) Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. *Journal of Heredity*, **89**, 438–450.
- Waser PM, Strobeck C (1998) Genetic signatures of interpopulation dispersal. *Trends in Ecology and Evolution*, **13**, 43–44.
- Wood CC, Foote CJ, Rutherford DT (1999) Ecological interactions between juveniles of reproductively isolated anadromous and non-anadromous morphs of sockeye salmon, *Oncorhynchus nerka*, sharing the same nursery lake. *Environmental Biology of Fishes*, **54**, 161–173.
- Wood CC, McKinnell S, Mulligan TJ, Fournier DA (1987) Stock identification with the maximum-likelihood mixture model: sensitivity analysis and application to complex problems. *Canadian Journal of Fisheries and Aquatic Sciences*, **44**, 866–881.
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