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# Interplay between ecological, behavioural and historical factors in shaping the genetic structure of sympatric walleye populations (*Sander vitreus*)

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**Abstract**

**Disentangling ecological, behavioural and evolutionary factors responsible for the presence of stable population structure within wild populations has long been challenging to population geneticists. This study primarily aimed at decoding population structure of wild walleye (*Sander vitreus*) populations of Mistassini Lake (Québec, Canada) in order to define source populations to be used for the study of spatial partitioning using individual-based multilocus assignment methods, and decipher the dynamics of individual dispersal and resulting patterns of spatial resource partitioning and connectivity among populations. A second objective was to elucidate the relationships between biological characteristics (sex, size, age and population of origin) and an individual's probability to migrate and/or disperse. To do so, a total of 780 spawning individuals caught on five distinct spawning sites, and 1165 postspawning individuals, captured over two sampling seasons (2002–2003) were analysed by means of eight microsatellite loci. Four temporally stable walleye populations associated with distinct reproductive grounds were detected. These populations were differentially distributed among lake sectors during their feeding migration and their spatial distribution was stable over the two sampling seasons. Dispersing individuals were identified ($n$ = 61); these revealed asymmetrical patterns of dispersal between populations, which was also confirmed by divergent admixture proportions. Regression models underlined population of origin as the only factor explaining differential dispersal of individuals among populations. An analysis of covariance (ANCOVA) indicated that larger individuals tended to migrate from their river of origin further away in the lake relative to smaller fish. In summary, this study underlined the relevance of using individual-based assignment methods for deciphering dynamics of connectivity among wild populations, especially regarding behavioural mechanisms such as differential spatial partitioning and dispersal responsible for the maintenance of genetic population structure.**

*Keywords*: asymmetrical dispersal, feeding migration, population assignment, sex-biased-dispersal, spatial distribution, spatial resource partitioning

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## Introduction

Understanding the dynamics of population connectivity is essential towards the management and conservation of wild species, as such processes directly relate to the probability of occurrence of individuals, both temporally and spatially (Clobert *et al*. 2001). Dispersal, as well as migration between reproductive and feeding sites, plays an important role in defining patterns of population structure and local adaptations (Whitlock 2001). In aquatic organisms such as fish, documenting behavioural parameters through direct observations has often been logistically challenging and consequently, knowledge regarding the dynamics of dispersal and resource partitioning in fish has been more limited than for other vertebrates. For example, sex-biased dispersal has been extensively studied in mammals, where females tend to be the philopatric sex

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(Wolff 1997), and birds show the reversed trend (Wolff & Plissner 1998; Clarke & Low 2001), although exceptions have been reported for both groups (Clarke *et al*. 1997; Favre *et al*. 1997; Dallimer *et al*. 2002). In contrast, sex-biased dispersal in fishes has rarely been studied (but see Hansen *et al*. 2001; Hutchings & Gerber 2002; Fraser *et al*. 2004). Similarly, the dynamics of spatial and temporal resource partitioning among fish populations has received little attention relative to terrestrial vertebrates (but see Taylor *et al*. 1997; Turgeon *et al*. 1999; Potvin & Bernatchez 2001; Fraser & Bernatchez 2005a), except for the classical dichotomy between benthic and limnetic trophic ecotypes (Schluter 2001).

Individual-based multiloci analyses offer the potential for improving our understanding of the dynamics of population interactions by allowing 'real-time' estimates of asymmetrical dispersal (Paetkau *et al*. 2004) in relation to individual phenotypic characteristics (Aars & Ims 2000; Fraser *et al*. 2004). In fishes, these techniques allowed documenting the differential use of lacustrine habitat by individuals belonging to genetically distinct populations (Potvin & Bernatchez 2001), and showing phenotypic differences adapted to the differential use of these habitats (Fraser & Bernatchez 2005a). These approaches may also allow assessing the extent of movement actually translated into gene flow estimates between populations, a key element towards understanding metapopulation processes (Pannel & Charlesworth 2000; Jehle *et al*. 2005).

The walleye (*Sander vitreus*), a member of the percid family broadly distributed throughout the northern part of North America, is of particular interest for studying the dynamics of population interactions. The species shows a propensity for both philopatry (Jennings *et al*. 1996; Stepien & Faber 1998), and long-distance dispersal (Wolfert 1969), yet knowledge about the consequences of these behaviours on population structure are unknown. Similarly, there have been very few studies documenting determinants of dispersal and migration in walleye, and results were contradictory, particularly as it relates to the occurrence or not of sex-biased dispersal (Stepien & Faber 1998; McParland *et al*. 1999). Finally, most of walleye research has taken place in the Laurentian Great Lakes (Billington & Hebert 1988; Ward *et al*. 1989; Todd 1990; Billington & Strange 1995; Gatt *et al*. 2002) where populations are strongly exploited by angling and commercially, and have been heavily stocked. Mistassini Lake, a large (2150 km$^2$) oligotrophic postglacial lake located in central Québec, Canada (Fig. 1), represents a pristine habitat for walleye. Being geographically remote, not heavily exploited, and never stocked, its ecological integrity has not been altered as extensively as more southern walleye habitats. Moreover, the range of geographical distances between relatively few sites for reproduction (from 10 to over 150 km), makes this system particularly useful for comparing patterns of dispersal, as well as documenting its impact on the extent of differentiation between populations. Mistassini Lake has also been the theatre of extensive research concerning genetic structure and population dynamics of brook charr (*Salvelinus fontinalis*), which allows us to contrast patterns of population structuring between species with very distinct life histories, but sharing a same environment.

The first objective of this study was to document patterns of genetic population structure in walleye from Mistassini

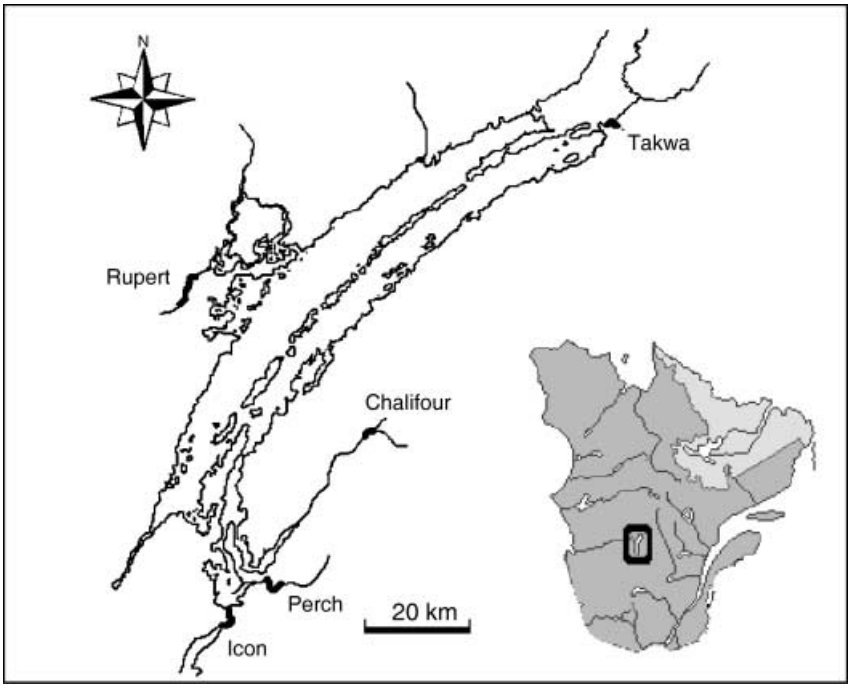


**Fig. 1** Location map of Mistassini Lake (inset map) tributaries (Icon, Perch, Chalifour, and Takwa rivers), and outflow (Rupert River) that were sampled in 2002 and 2003.

Lake in order to: (i) define source populations to be used for the study of spatial partitioning by means of individual-based multilocus assignment methods, and (ii) decipher the dynamics of individual dispersal, lake migration and resulting patterns of spatial resource partitioning and connectivity among populations. A second objective was to investigate the relationships between individual biological characteristics (sex, size, age and population of origin), dispersal and lake migration. Here dispersal refers to movements of adult fish between spawning grounds found in lake tributaries and associated with genetically distinct populations, whereas lake migration refers to movements of fish from their native spawning grounds to different lake sectors for feeding during the summer period. Theory and empirical observations in other species suggests that male-biased dispersal is often associated to polyandrous systems where access to females is limited, whereas female biased-dispersal is associated to monogamous systems where material resources are limiting (Perrin & Goudet 2001). Walleye are broadcast spawners, neither build nests nor hold territories, and spawning females may mate with up to six males (Scott & Crossman 1973). We therefore predicted that male-biased dispersal should predominate in this species. Wolfert (1963) also showed a tendency for older walleyes to move more extensively than younger fish. Consequently, we hypothesized that age and size were more likely to influence dispersal relative to other traits.

Finally, we compare and discuss the patterns of population structure, dispersal and lake migration observed for walleye with those we documented recently for Mistassini Lake brook charr (Fraser *et al*. 2004; Fraser & Bernatchez 2005a). Given the paucity of published studies dealing with determinism of dispersal and the dynamics of spatial and temporal resource partitioning among sympatric fish populations (other than the dichotomy between benthic and limnetic trophic ecotypes), as well as the sympatric occurrence of both species in Mistassini Lake and their very distinct life history and behavioural characteristics, this comparison offers an opportunity to improve current knowledge on this particular issue.

## Material and methods

### *Sampling*

Information about the localization of major spawning sites was gathered through interviews with local experts from the Cree First Nation of Mistassini. Five major spawning sites were identified, including four tributaries; Perch and Icon, in the south, Chalifour in the southwest, Takwa in the north, and the Rupert, the lake outflow (Fig. 1). A total of 780 adult fish comprising two temporal replicates for all sites were caught by angling and gillnetting over the spring of 2002 and 2003. A second sampling session took place during the feeding period (July–August) of both years for collecting individuals captured by traditional fishermen and anglers in the lake. A total of 1165 fish (624 in 2002 and 541 in 2003) were sampled from more than 30 locations covering lake sectors known by local people to be used by walleye. Overall, 1945 fish were sampled. Pectoral fin clips were nonlethally removed and preserved in 95% ethanol until DNA extraction using MultiScreen lysate clearing plates and MultiScreen$_{96}$ BAC plates from Montage BAC$_{96}$ Miniprep Kit (Millipore Co.). A total of 1083 fish could be sexed, 926 measured and 928 weighted, and 452 randomly selected fish were sacrificed for ageing using the opercular bone, including 189 fish from the spawning grounds and 263 from the lake.

### *Genetic analyses*

Samples were screened for variation at 10 microsatellite loci. Multiplex polymerase chain reaction (PCR) amplifications were performed for five loci developed for walleye (Svi L2, Svi L3, Svi L6, Svi L8, Svi L11) (Wirth *et al*. 1999) and one for yellow perch *Perca flavescens* (Pfla 2, Leclerc *et al*. 2000), PCRs were performed in 20-μL reaction volume containing 2 μL of 10× reaction buffer (10 mM Tris-HCl pH 9.0, 1% Triton X-100, 50 mM KCl, 1.0 mM $MgCl_2$); 0.8 μL of dNTP (10 mM each); 0.4 U of *Taq* polymerase; 0.9 μL, 0.6 μL, 0.3 μL, 0.15 μL, 0.35 μL, and 0.6 μL, respectively, of the forward and reverse primers mentioned above (10 pmol each), and 50–100 ng DNA template. PCR included an initial denaturation step of 3 min at 95 °C, followed by 40 cycles of 30 s at 96 °C, 30 s at 53 °C and 30 s at 72 °C, completed with 5-min final elongation at 72 °C. PCR products were purified using Millipore's PCR$_{96}$ cleanup protocol, and were separated by electrophoresis using an MJ Research Base Station automated sequencer and scored using the software CARTOGRAPHER (MJ Research Inc.). An additional set of four loci were screened, three developed for walleye (Svi L4, Svi L17 and Svi L26) (Borer *et al*. 1999), and Cv09 developed for the striped darter *Etheostoma virgatum* (Porter *et al*. 2002). Amplifications were performed as simplex according to Borer *et al*. (1999) and Porter *et al*. (2002), and PCR products were pooled and separated with a 3100 ABI sequencer and scored using GENOTYPER 3.7 and GENESCAN 3.7.1. (Applied Biosystems Inc.).

### *Genetic diversity*

Within-population diversity was estimated using standard descriptive statistics: number of alleles per locus ($A$), expected ($H_E$) and observed ($H_O$) heterozygosities. Hardy–Weinberg equilibrium (HWE) concordance was tested using the permutation test implemented in GENETIX 4.02 (Belkhir *et al*. 2001). Linkage disequilibrium (LD) tests were performed using GENEPOP 3.3 (Raymond & Rousset 1995).

Sequential Bonferroni corrections for multiple tests were applied to maintain the table-wide significance level to $\alpha = 0.05$ (Rice 1989). A Kendall coefficient of concordance rank test was performed on $F_{IS}$ values in cases where deviations from HWE were detected in order to identify the source of disequilibrium (e.g. over all loci or locus specific) (David *et al*. 1997; Rogers & Curry 2004).

### *Genetic structure and temporal stability*

The level of genic differentiation ($G$) (Guo & Thompson 1992) was estimated for each locus and globally over all loci (Ryman & Jorde 2001) between all pairs of samples using GENEPOP 3.3 (Raymond & Rousset 1995). We also computed pairwise $F_{ST}$ values using Weir & Cockerham (1984) θ estimator, as well as $R_{ST}$ values (Michalakis & Excoffier 1996). Hardy *et al*. (2003) test was performed, where global and pairwise $F_{ST}$ and $R_{ST}$ estimates were computed to provide a simulated distribution of $R_{ST}$ values ($\rho R_{ST}$). In a situation where $R_{ST}$ is equivalent to $F_{ST}$, drift is most likely the source of differentiation and $F_{ST}$ should be used. On the other hand, when $R_{ST}$ is higher than $F_{ST}$, mutation predominates and $R$ statistics becomes a less biased estimator (Slatkin 1995).

In order to assess the temporal stability of the observed genetic structure, a genetic distance unrooted neighbour-joining tree was first constructed using Cavalli-Sforza & Edwards (1967) chord distance ($D_{ce}$) with bootstrap values obtained over 5000 replicates using POPULATION 1.2.14 (Langella 2001) and visualized in TREEVIEW (Page 1996). An analysis of molecular variance (AMOVA) was also performed using ARLEQUIN 2.0 (Schneider *et al*. 2000) in order to decompose the molecular variance component attributable to the differentiation among populations, between sampling years within population, and between individuals within populations. A third method consisted in comparing $G$ an $F_{ST}$ values (as described above) between temporal samples. Since temporal variation was negligible relative to spatial variation (see Results), temporal samples were pooled by sampling site for all subsequent analyses.

The program STRUCTURE version 2.0 (Pritchard *et al*. 2000) was used to verify clustering assumptions inferred by conventional analyses. We tested the probability that the submitted samples were composed of $k = 1$–7 populations doing 3 iterations per values (150 000 burn-in, 550 000 Markov chain Monte Carlo) with a model assuming admixture and correlated allele frequencies between groups. We subsequently used the most likely iteration to visualize the genetic composition of the putative populations by averaging the individual admixture proportions $Q$, which represents the proportion of an individual's genome that originates from each of the potential populations of origin (Pritchard *et al*. 2000). Individuals of unknown origin as well as first generation migrants were excluded from this analysis (see below).

### *Population assignment, dispersal, and spatio-temporal distribution of populations*

Samples caught on spawning grounds were used to create unbiased baseline populations. Since no significant genetic differentiation was found between them (see Results), samples from Perch and Icon were pooled into a group called 'Perch–Icon' thereafter, which also contributed to increase assignment precision by reducing the number of putative population of origin (Hansen *et al*. 2001; Baudouin *et al*. 2004). Similarly, pooling temporal samples for each site increased the accuracy of allele frequency distributions by increasing sample size (Cornuet *et al*. 1999). Individuals of unknown origin were first identified using Rannala & Mountain's (1997) Bayesian assignment criteria coupled with Paetkau *et al*. (2004) simulation algorithm (10 000 simulated individuals) implemented in GENECLASS 2 (Piry *et al*. 2004) and these were removed from baseline populations for subsequent analyses. With the same software, we used the first generation migrant detection option (10 000 simulated individuals) to distinguish dispersers from resident fish (Paetkau *et al*. 2004). Since these dispersers were caught during reproduction, they have not contributed to the actual distribution of allelic frequencies. Therefore, they were excluded from the population assignment baseline populations in order to maximize the discriminating power of the assignment procedure. Finally, Rannala & Mountain's (1997) Bayesian assignment criteria was used to reassign baseline populations' individuals to their population of origin and thereby inferring the discriminatory capacity of reference populations in assigning fish of unknown origin.

Mistassini Lake was divided into four sectors for the purpose of spatial partitioning analysis (Fig. 5). These sectors were defined on the basis of both management and physical criteria. Thus, the open water section of the lake was divided into two sectors (North, South) separated by the 51st parallel. In the current management practice, access to the northern sector is only granted to the Cree First Nation fishers. The other two sectors, the Rupert mouth and Baie-du-Poste are partly closed physical entities but are linked to the main lake by channels up to 1 km wide and therefore allowing fish movements. Fish captured in these sectors during the harvesting season of 2002 ($n = 623$) and 2003 ($n = 541$) were assigned to their putative population of origin using Rannala & Mountain's (1997) Bayesian assignment criteria. This information was subsequently used to document the spatial use of the lake based on their distribution among the predefined sectors, and to evaluate the relative contribution of each population to the mixed-stock fishery. This was achieved by performing a maximum-likelihood analysis of variance (ANOVA) to decompose the variance components attributable to the variation between years within sector and between sectors.

We also contrasted the relative proportions of each population between both sampling years within a sector, independently from the other sectors, using a chi-square test.

### *Individual basis underlining dispersal*

We tested whether individual characteristics of sex, age, total length, weight and population of origin could explain observed patterns of dispersal between populations. Univariate statistics were used to explore the individual effect of all variables on the dependant variable dispersal. Chi-squared tests were used for categorical variables sex (male or female, $N = 684$) and population of origin (Perch–Icon, Chalifour, Takwa and Rupert, $N = 774$). *T*-tests were used for continuous variables, including age ($N = 180$), total length ($N = 516$) and weight ($N = 514$). Since population of origin had a significant effect on dispersal (see Results), we performed chi-squared tests on all pairs of population in order to decipher the global contingency table and underline the statistical significance of differential dispersal among the four populations. Significance levels were fixed at $\alpha = 0.05$ for all analyses.

For comparative purposes, Favre *et al*. (1997) assignment index method was used to test for sex-biased dispersal. Thus, spawning individuals were reassigned to their putative population of origin using Paetkau *et al*. (1995) frequency-based assignment criteria implemented in GENECLASS 2 (Piry *et al*. 2004). Excluded individuals and identified dispersers were removed from the reference file in order to maximize assignment precision (see population assignment method section). Assignment index values were computed for each individual (see Mossman & Waser 1999 or Favre *et al*. 1997). Population means were substracted from assignment index values after log transformation in order to correct for population effects. Negative values characterize individuals showing a lower probability to be born locally. Means for grouped males and females were compared globally (all populations pooled) and for each individual population using nonparametric Mann–Whitney *U*-tests.

### *Individual basis underlining patterns of feeding migration*

Population assignment procedure combined with geographical positioning of captured fish was used to estimate the distance of lacustrine feeding migration for 411 individuals. More specifically, we tested the effect of variables sex, age, length, weight and population of origin on lake migration distances. We used migration distance as the dependant variable in an analysis of covariance (ANCOVA, SAS, 'proc. Mixed') for testing if sex, length, population of origin and pairwise interactions could significantly explain this parameter. We first created a complete model and then discarded nonsignificant parameters until obtaining a final model that included only significant parameters. Significance levels were fixed at $\alpha = 0.05$ for all analyses.

## Results

### *Genetic diversity*

Pronounced deficits in heterozygotes were observed for Pfla *2*, and scoring problems were frequent for Svi L6 (Table 1). Therefore, these two loci were discarded from all analyses. Svi 8 and Svi 11 presented significant departure from HWE, but Kendall coefficient of concordance rank test revealed that the trend for heterozygote deficiencies at these loci was not significant over all populations (Kendall's coefficient of concordance = 0.176; average rank $r = 0.084$; $P = 0.09$). Fisher's exact test for linkage disequilibrium between each pair of loci across all populations revealed only one significant relationship (Svi 2 and Svi 11) observed in the Chalifour sample, suggesting the absence of overall allelic covariance between these pairs of loci across all populations (Austin *et al*. 2004).

### *Genetic structure and temporal stability*

The comparison between $R_{ST}$ and simulated values ($\rho R_{ST}$) was not significant ($P = 0.44$), and therefore only *F*-statistics were retained for subsequent analyses. Except for three pairwise comparisons, pairwise *G* and $\theta$ calculations revealed significant genetic structuring between sampling sites (Table 2). No significant differentiation was observed between Perch and Icon. Moreover, the extent of differentiation between these two sites and Chalifour was low, with $\theta$ values ranging from 0017 to 0.028. The overall genic differentiation between Chalifour and Icon was not significant in 2002. The level of differentiation between Chalifour and Takwa was intermediate ($\theta$ values = 0.031 for 2002 and 0.033 for 2003), while the discrepancy between Takwa and other locations was more pronounced ($\theta$ values ranging between 0.031 and 0.067). Finally, all pairwise tests including Rupert showed the highest and most significant level of differentiation with $\theta$ ranging from 0.045 to 0.079. The population tree ($D_{ce}$, Fig. 2) corroborated this pattern of differentiation, regrouping geographical and temporal samples into four distinct groups: Rupert being the most distant, Takwa being intermediate between Rupert and the southern sites (Chalifour, Perch and Icon), the latter two sites clustering into a single group. In all cases, temporal samples at a given site clustered together with high bootstrap support (96–100%). Overall, these results suggested the existence of four temporally stable walleye populations in Lake Mistassini.

The AMOVA results further confirmed the temporal stability of the observed population structure. Although the analysis revealed significant differences between temporal samples (Table 3), the spatial component of genetic variance was 18.5

**Table 1** Descriptive statistics for five walleye spawning sites in Lake Mistassini. Measures are presented as follows: *N*, sample size; *A*, total number of alleles; $F_{IS}$, correlation value of heterozygote deficit; $H_E$, expected heterozygosity; and $H_O$, observed heterozygosity. Asterisks indicate loci showing significant deviation from Hardy–Weinberg equilibrium ($P = 0.05$). Loci Svi 6 and Pfla 2 were excluded from all analyses

| | | | 2002 | | | | | 2003 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Locus | *A* | | Perch | Icon | Chalifour | Rupert | Takwa | Perch | Icon | Chalifour | Rupert | Takwa |
| Svi 2 | 7 | *N* | 61 | 33 | 101 | 52 | 79 | 95 | 82 | 35 | 50 | 62 |
| | | *A* | 5 | 6 | 6 | 4 | 4 | 6 | 6 | 5 | 4 | 5 |
| | | $F_{IS}$ | −0.010 | 0.113 | −0.094 | 0.064 | 0.126 | −0.036 | 0.071 | −0.086 | −0.033 | 0.264 |
| | | $H_E$ | 0.69 | 0.74 | 0.66 | 0.69 | 0.59 | 0.71 | 0.70 | 0.65 | 0.67 | 0.59 |
| | | $H_O$ | 0.70 | 0.67 | 0.72 | 0.65 | 0.52 | 0.73 | 0.66 | 0.71 | 0.70 | 0.44 |
| Svi 3 | 23 | *N* | 61 | 33 | 109 | 61 | 91 | 94 | 82 | 71 | 72 | 85 |
| | | *A* | 11 | 10 | 15 | 17 | 14 | 14 | 12 | 14 | 16 | 15 |
| | | $F_{IS}$ | 0.070 | 0.012 | 0.018 | 0.023 | −0.030 | − 0.172 | 0.046 | 0.032 | 0.023 | 0.014 |
| | | $H_E$ | 0.68 | 0.73 | 0.77 | 0.87 | 0.74 | 0.75 | 0.72 | 0.77 | 0.87 | 0.70 |
| | | $H_O$ | 0.64 | 0.73 | 0.76 | 0.87 | 0.77 | 0.88 | 0.70 | 0.75 | 0.86 | 0.69 |
| Svi 4 | 6 | *N* | 61 | 33 | 109 | 61 | 94 | 94 | 85 | 71 | 79 | 91 |
| | | *A* | 5 | 4 | 5 | 5 | 5 | 5 | 5.00 | 5 | 4 | 5 |
| | | $F_{IS}$ | 0.027 | −0.148 | −0.036 | 0.021 | 0.040 | 0.064 | −0.009 | 0.003 | 0.000 | −0.044 |
| | | $H_E$ | 0.35 | 0.44 | 0.50 | 0.49 | 0.43 | 0.32 | 0.27 | 0.55 | 0.52 | 0.48 |
| | | $H_O$ | 0.34 | 0.52 | 0.52 | 0.49 | 0.41 | 0.30 | 0.27 | 0.55 | 0.52 | 0.51 |
| Svi 6* | 7 | *N* | 61 | 33 | 107 | 54 | 94 | 95 | 84 | 71 | 78 | 84 |
| | | *A* | 5 | 5 | 7 | 6 | 6 | 7 | 7 | 7 | 5 | 7 |
| | | $F_{IS}$ | 0.129 | 0.048 | 0.102 | 0.181 | 0.111 | 0.166 | −0.040 | 0.117 | 0.191 | 0.045 |
| | | $H_E$ | 0.76 | 0.75 | 0.77 | 0.72 | 0.76 | 0.83 | 0.77 | 0.78 | 0.52 | 0.74 |
| | | $H_O$ | 0.67 | 0.73 | 0.81 | 0.59 | 0.68 | 0.69 | 0.81 | 0.69 | 0.48 | 0.71 |
| Svi 8* | 15 | *N* | 61 | 33 | 106 | 59 | 91 | 94 | 85 | 71 | 77 | 89 |
| | | *A* | 6 | 6 | 8 | 8 | 7 | 6 | 6 | 9 | 6 | 14 |
| | | $F_{IS}$ | −0.019 | 0.060 | 0.011 | 0.101 | 0.252 | 0.194 | −0.069 | 0.124 | 0.049 | 0.303 |
| | | $H_E$ | 0.69 | 0.70 | 0.62 | 0.49 | 0.41 | 0.71 | 0.73 | 0.67 | 0.49 | 0.45 |
| | | $H_O$ | 0.70 | 0.67 | 0.61 | 0.44 | 0.31 | 0.57 | 0.79 | 0.59 | 0.47 | 0.31 |
| Svi 11* | 15 | *N* | 61.00 | 32 | 107 | 60 | 92 | 96 | 85 | 71 | 79 | 90 |
| | | *A* | 7 | 7 | 10 | 7 | 8 | 7 | 7 | 8 | 7 | 9 |
| | | $F_{IS}$ | 0.099 | 0.172 | 0.235 | 0.132 | −0.030 | −0.076 | −0.056 | 0.075 | 0.108 | 0.080 |
| | | $H_E$ | 0.70 | 0.74 | 0.75 | 0.52 | 0.55 | 0.70 | 0.71 | 0.76 | 0.52 | 0.56 |
| | | $H_O$ | 0.64 | 0.63 | 0.58 | 0.47 | 0.57 | 0.76 | 0.75 | 0.70 | 0.47 | 0.52 |
| Svi 17 | 6 | *N* | 61 | 33 | 109 | 61 | 94 | 96 | 85 | 71.00 | 79 | 90 |
| | | *A* | 4 | 4 | 4 | 5 | 4 | 4 | 5 | 4 | 6 | 5 |
| | | $F_{IS}$ | −0.005 | −0.128 | −0.033 | 0.141 | −0.017 | −0.033 | −0.181 | −0.145 | −0.090 | −0.001 |
| | | $H_E$ | 0.65 | 0.66 | 0.64 | 0.68 | 0.55 | 0.64 | 0.61 | 0.60 | 0.69 | 0.54 |
| | | $H_O$ | 0.66 | 0.76 | 0.60 | 0.59 | 0.56 | 0.67 | 0.73 | 0.69 | 0.76 | 0.54 |
| Svi 26 | 16 | *N* | 61 | 33 | 109 | 61 | 94 | 96 | 85 | 70 | 79 | 91 |
| | | *A* | 8 | 7 | 8.00 | 9 | 7 | 10 | 9 | 6 | 7 | 9 |
| | | $F_{IS}$ | −0.015 | −0.044 | −0.02 | 0.085 | −0.016 | 0.013 | −0.072 | −0.242 | −0.031 | 0.051 |
| | | $H_E$ | 0.48 | 0.46 | 0.51 | 0.71 | 0.57 | 0.49 | 0.40 | 0.45 | 0.62 | 0.64 |
| | | $H_O$ | 0.49 | 0.48 | 0.52 | 0.66 | 0.59 | 0.49 | 0.44 | 0.56 | 0.65 | 0.62 |
| Pfla 2* | 19 | *N* | 61 | 33 | 107 | 61 | 89 | 94 | 79 | 68 | 78 | 89 |
| | | *A* | 7 | 8 | 10 | 7 | 12 | 10 | 9 | 10 | 11 | 11 |
| | | $F_{IS}$ | 0.308 | 0.604 | 0.315 | 0.351 | 0.227 | 0.219 | 0.252 | 0.444 | 0.118 | 0.312 |
| | | $H_E$ | 0.73 | 0.75 | 0.68 | 0.77 | 0.75 | 0.72 | 0.65 | 0.73 | 0.75 | 0.73 |
| | | $H_O$ | 0.51 | 0.30 | 0.47 | 0.51 | 0.58 | 0.56 | 0.49 | 0.41 | 0.67 | 0.51 |
| CV 09 | 23 | *N* | 60 | 33.00 | 109 | 61 | 94 | 95 | 85 | 71 | 79 | 82 |
| | | *A* | 9 | 8 | 5 | 11 | 8 | 13 | 13 | 6 | 12 | 7 |
| | | $F_{IS}$ | −0.104 | 0.114 | −0.042 | 0.005 | 0.041 | −0.027 | −0.017 | 0.024 | 0.025 | 0.081 |
| | | $H_E$ | 0.69 | 0.74 | 0.64 | 0.8 | 0.62 | 0.71 | 0.71 | 0.62 | 0.80 | 0.48 |
| | | $H_O$ | 0.77 | 0.67 | 0.67 | 0.8 | 0.57 | 0.74 | 0.73 | 0.61 | 0.78 | 0.51 |
| All loci | | N | 61 | 33 | 109 | 61 | 94 | 96 | 85 | 71 | 79 | 91 |
| | | $\bar{A}$ | 6.9 | 6.5 | 7.6 | 8.3 | 7.1 | 8.1 | 8.0 | 7.1 | 7.8 | 8.6 |
| | | $H_E$ | 0.62 | 0.65 | 0.64 | 0.65 | 0.56 | 0.63 | 0.61 | 0.63 | 0.65 | 0.57 |
| | | $H_O$ | 0.62 | 0.64 | 0.62 | 0.62 | 0.54 | 0.64 | 0.63 | 0.64 | 0.65 | 0.53 |

**Table 2** Spatial and temporal pairwise comparisons of genetic differentiation between Mistassini walleye spawning sites. Genic differentiation (*G*) is represented by the number of loci showing significant deviation in allelic frequencies. * = $P < 0.01$; ** $P < 0.001$

| | 2002 | | 2003 | |
|---|---|---|---|---|
| Spawning sites comparisons | θ | *G* | θ | *G* |
| Perch vs. Icon | −0.003 | 0 | 0.003 | 1 |
| Perch vs. Chalifour | 0.017 | 4** | 0.025 | 7** |
| Perch vs. Rupert | 0.069 | 8** | 0.064 | 8** |
| Perch vs. Takwa | 0.049 | 8** | 0.051 | 8** |
| Icon vs. Chalifour | 0.017 | 4 | 0.028 | 6** |
| Icon vs. Rupert | 0.055 | 6** | 0.079 | 8** |
| Icon vs. Takwa | 0.058 | 8** | 0.067 | 8** |
| Chalifour vs. Rupert | 0.052 | 8** | 0.06 | 8** |
| Chalifour vs. Takwa | 0.031 | 8** | 0.033 | 7** |
| Rupert vs. Takwa | 0.047 | 7** | 0.045 | 6** |

| | 2002 vs. 2003 | |
|---|---|---|
| Temporal comparisons | θ | *G* |
| Perch | 0.003 | 1* |
| Icon | 0.0029 | 0 |
| Chalifour | 0.0017 | 1 |
| Rupert | 0.0003 | 3** |
| Takwa | 0.0017 | |

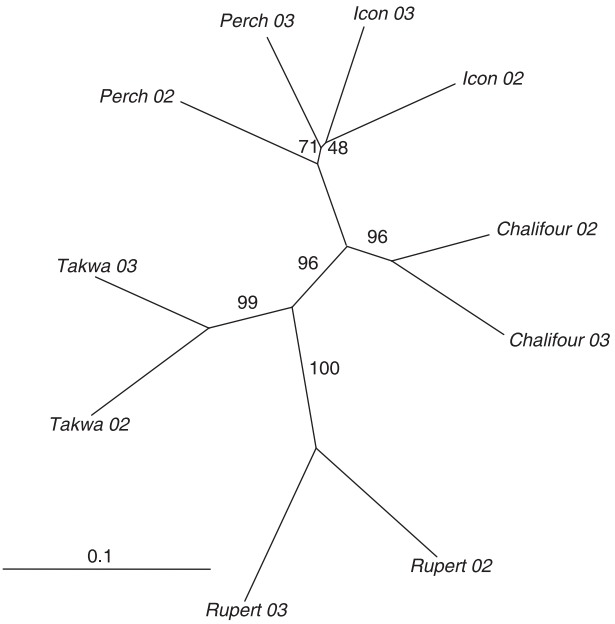


**Fig. 2** Unrooted neighbour-joining tree of five Mistassini Lake walleye spawning sites for sampling years 2002 (02) and 2003 (03) using eight microsatellite loci and based on Cavalli-Sforza & Edwards (1967) chord-distance ($D_{ce}$). Genotypic data were bootstrapped over loci with replacement and 5000 replicates. The numbers represent the percent support of groupings.

times more important than temporal variation within site. Similarly, STRUCTURE clustering analyses resolved four distinct groups ($k = 4$, three iterations with posterior probability > 0.999), which corroborated the existence of four genetically distinct and temporally stable populations in Lake Mistassini.

### *Population assignment and dispersal*

Exclusion tests performed on fish caught on spawning grounds identified six individuals of unknown origin, which were randomly distributed throughout spawning aggregations. A total of 61 fish were classified as first generation migrants: 26 from the Perch–Icon population, 15 from Chalifour, 14 from Takwa, and only 6 from Rupert. Even tough there were no overall significant differences in the frequencies of migrants (number of fish identified as migrants in a population/total number of fish sampled in that population) captured between populations ($\chi^2 = 3.44$, $P = 0.329$), pairwise comparisons showed a marginally significant difference between Rupert and Perch–Icon ($\chi^2 = 3.386$, $P = 0.066$). Information about gender was available for 54 out of the 61 identified migrants (39 males and 15 females), which was not different than the observed sex ratio among nonmigrants (data not shown).

The assignment procedure (source towards source) performed on the 713 remaining samples revealed an assignment success that varied between 76% and 89% depending on populations, for an overall success rate of 84% (Table 4). The level of introgression for all four populations was approximated from the analysis of admixture proportions performed with STRUCTURE. The southern populations Perch–Icon and Chalifour showed the highest levels of admixture (52–53%, respectively), Rupert showed the lowest (27%), and Takwa was intermediate (41%) (Fig. 3).

### *Spatiotemporal distribution of populations within lake*

Exclusion tests performed on mixed-stock samples from the lake identified 13 fish of unknown origin in the 2002

**Table 3** Partitioning of molecular variance (AMOVA) among the four walleye populations of Mistassini Lake. Hierarchical levels are partitioned temporally (between sampling years within populations) and spatially (among populations and within population in each year)

| Variance component | d.f. | Percentage variation | *P* |
|---|---|---|---|
| Among populations | 3 | 4.45 | 0.0000 |
| Among years within population | 4 | 0.24 | 0.0137 |
| Between individuals within population | 1552 | 95.31 | 0.0088 |

**Table 4** Distribution of individuals of unknown origin, first generation migrants, and summary of individual reassignment (source towards source) of mature fish caught on the spawning sites of the four walleye populations of Mistassini Lake

| | Capture site | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Perch-Icon | | Chalifour | | Rupert | | Takwa | |
| Site of assignment | Migrants | Assigned to | Migrants | Assigned to | Migrants | Assigned to | Migrants | Assigned to |
| Perch-Icon | | 83.5% (207) | 5 | 15.3% (25) | 1 | 3.0% (4) | 9 | 5.3% (9) |
| Chalifour | 15 | 12.1% (30) | | 76.1% (124) | 3 | 2.3% (3) | 4 | 4.7% (8) |
| Rupert | 0 | 1.2% (3) | 4 | 1.2% (2) | | 89.4% (118) | 1 | 4.7% (8) |
| Takwa | 11 | 3.2% (8) | 6 | 7.4% (12) | 2 | 5.3% (7) | | 85.3% (145) |
| Total | 26 | 248 | 15 | 163 | 6 | 132 | 14 | 170 |
| Unknown origin | 1 | | 2 | | 2 | | 1 | |

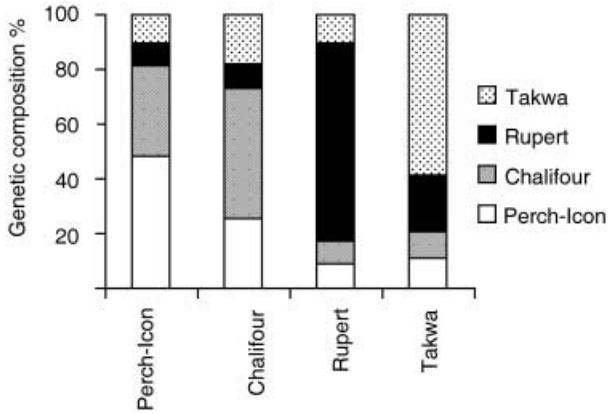


**Fig. 3** Graphical visualization of averaged individual admixture proportions ($Q$, $k$ = four populations, STRUCTURE 2.0, Pritchard *et al*. 2000) found within Mistassini Lake walleye populations.

samples and only one in 2003. Assignment of the mixed-stock samples to their population of origin showed that the Takwa population was the main contributor in Lake Mistassini with 38.0% and 42.2% of all sampled fish in 2002 and 2003, respectively (Table 5). The contribution of the Rupert population was the lowest, representing only 10.9% and 14.8% of all fish collected in the lake. The maximum-likelihood ANOVA revealed only a marginally significant difference in the relative representation of each population ($\chi^2 = 7.6$, $P = 0.056$) between temporal samples, whereas a highly significant difference was detected among sectors ($\chi^2 = 393.71$, $P < 0.0001$). The proportions of different populations observed in the two open water sectors North and South were similar, with Takwa being the most important contributor in both. The other two sectors Rupert and Baie-du-Poste were dominated by fish originating from spawning grounds associated with rivers draining into these sectors (Fig. 5).

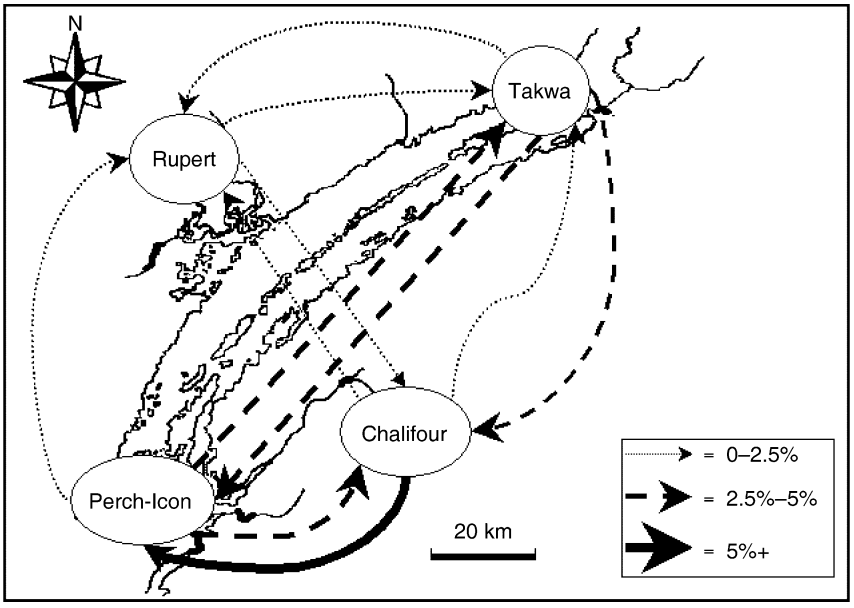


**Fig. 4** Schematic representation of differential ratios of real-time dispersal estimates between sampled populations: Perch–Icon, Chalifour, Rupert, and Takwa. Thick plain arrows; dispersal ratios (number of dispersers/total number of sampled fish) greater than 5%, broken line arrows; intermediate levels of dispersion (2.5–5%), small dotted arrows; low dispersal ratios (between 0 and 2.5%).

**Table 5** Numbers and proportion (in percent) of individuals assigned and excluded (unknown) for walleye sampled during summer feeding period of 2002 and 2003 in the lake

| | 2002 | | 2003 | |
|---|---|---|---|---|
| Population of assignment | *N* | % | *N* | % |
| Perch–Icon | 101 | 16.2 | 108 | 20 |
| Chalifour | 200 | 32.1 | 126 | 23.3 |
| Rupert | 68 | 10.9 | 80 | 14.8 |
| Takwa | 241 | 38.7 | 226 | 41.8 |
| Unknown | 13 | 2.1 | 1 | 0.002 |
| Total | 623 | 100 | 541 | 100 |

**Table 6** Pairwise comparisons of the proportion of migrants originating from each sampled populations. Lower matrix represents the absolute difference in proportion of migrants between pairs of populations (in per cent), and upper matrix represent *P* values ($\chi^2$) associated with pairwise differences. Asterisks underline significant differences ($\alpha = 0.05$)

| | Perch–Icon | Chalifour | Rupert | Takwa |
|---|---|---|---|---|
| Perch–Icon | | 0.019* | 0.371 | 0.084 |
| Chalifour | 5.50 | | 0.008* | 0.569 |
| Rupert | 0.80 | 6.96 | | 0.029* |
| Takwa | 2.99 | 0.32 | 4.78 | |

### *Individual characteristics and population of origin vs. dispersal*

Chi-squared tests revealed that walleye dispersal among reproductive sites did not differ between sexes ($\chi^2 = 0.39$, $P = 0.53$). On the other hand, the population of origin was significantly associated with dispersal ($\chi^2 = 10.42$, $P = 0.015$) (Fig. 4). In pairwise comparisons of populations, the proportion of dispersers originating from the Rupert population (3.65% of all the fish assigned to Rupert) was the lowest and significantly differed from the Chalifour (11.89%, $\chi^2 = 6.96$, $P = 0.008$), and Takwa (10.05%, $\chi^2 = 4.78$, $P = 0.029$) populations, but not from the Perch–Icon population (5.7%, $\chi^2 = 0.78$, $P = 0.371$). Perch–Icon showed lower proportions of dispersers relative to Takwa ($\chi^2 = 2.99$, $P = 0.084$), but differed from Chalifour ($\chi^2 = 5.49$, $P = 0.019$). Finally, Chalifour and Takwa did not differ in their proportion of assigned dispersers ($\chi^2 = 0.32$, $P = 0.569$) (Table 6). *T*-tests showed that neither age ($P = 0.234$), weight ($P = 0.992$), nor length ($P = 0.773$) was significantly associated to dispersal.

The assignment index for detecting sex-biased dispersal showed no significant differences between males and females values when all populations were pooled ($U = 453336{,}5$, $P = 0.78$) (Table 7). When compared independently, none of the populations showed significant differences (Perch–Icon $U = 7703$, $P = 0.92$; Chalifour $U = 1130{,}5$, $P = 0.40$; Rupert $U = 562$, $P = 0.64$; Takwa $U = 2237$, $P = 0.59$). Nevertheless, there was a trend in the data for mean corrected assignment index values to be lower for males than for females, both when all samples were pooled or considering populations separately, except for the Perch–Icon population (Table 7).

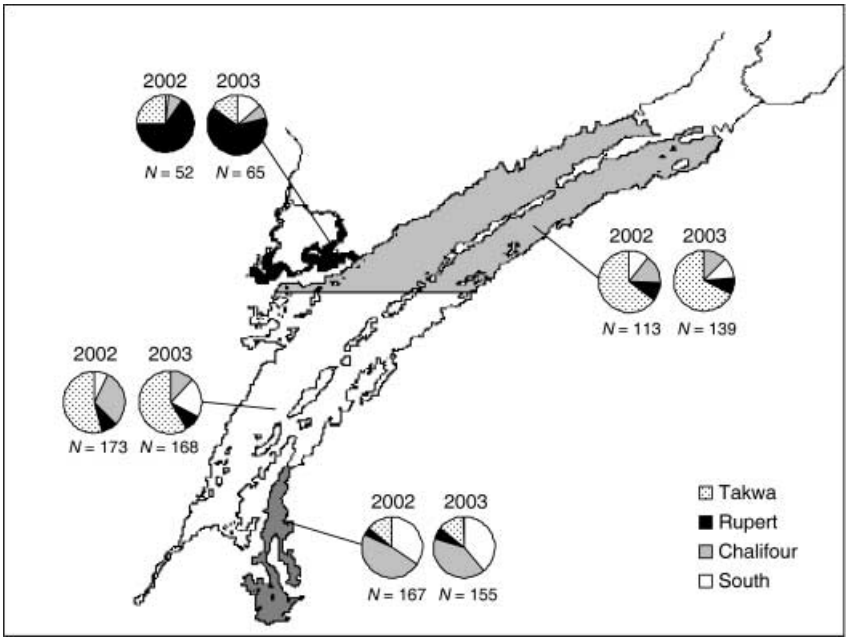


**Fig. 5** Spatial distribution of individually assigned Mistassini Lake walleye sampled within four sectors of the lake defined both by physical and management attributes (black, mouth of Rupert river; white, southern end of the lake; light grey, northern end of the lake; dark grey, Baie-du-Poste. Numbers below pie charts refer to the number of individuals analysed for each sampling year.

**Table 7** Mean (± SE) corrected assignment index values for the four walleye populations of Mistassini Lake and for all the populations pooled. Sample sizes are in ratio males to females

| | Sample size | Males | Females |
|---|---|---|---|
| Perch–Icon | 187:83 | 0.009 (0.103) | −0.045 (0.156) |
| Chalifour | 162:16 | −0.021 (0.123) | 0.210 (0.331) |
| Rupert | 43:28 | −0.221 (0.274) | −0.068 (0.327) |
| Takwa | 63:75 | −0.234 (0.224) | −0.023 (0.208) |
| Total (pooled) | 455:202 | −0.057 (0.073) | −0.020 (0.112) |

### *Individual characteristics, population of origin vs. lake migration*

Age, weight, and total length were highly correlated (Spearman's ρ ranging from 0.59 to 0.94, $P < 0.0001$). The correlation between total length and lake migration distance (Spearman's ρ = 0.094, $P = 0.057$) was higher than for weight (Spearman's ρ = 0.0558, $P = 0.259$) and age (Spearman's ρ = 0.092, $P = 0.155$). Therefore, total length was the only continuous variable included in the models. The final model of the covariance analysis integrated only two significant variables: population of origin and total length. The retained model explained 12% ($R^2 = 0.116$) of the total variance. Both fish length ($P = 0.0062$) and population of origin ($P < 0.0001$) had a significant effect on lake migration measured as the distance between the river of origin and individual geographical distribution within the lake. For all populations, larger walleye travelled significantly further than smaller ones in all four populations, sharing the same slope for total length (estimate = 0.072 ± 0.026). However, populations differed in their beta estimates (Rupert = 1.82 ± 0.44, Takwa = 4.03 ± 1.25, Perch-Icon = 4.57 ± 0.37, and Chalifour = 5.22 ± 0.33), which suggested population specific differences in behaviour associated with feeding migration in the lake. A difference of least squares means analysis was used to contrast populations in terms of differences in lake migratory distances. All pairwise comparisons including the Rupert population were highly significant ($P < 0.0001$), whereby migratory distances covered by fish from this population were lower than for any other populations. Chalifour and Takwa contrast was also significant ($P = 0.0003$), whereby lake migration was longer for the Takwa population, while contrasts between Perch–Icon and Chalifour ($P = 0.128$), and Perch–Icon and Takwa ($P = 0.137$) were not.

## Discussion

The primary objective of this study was to document patterns of genetic population structure in order to decipher the dynamics of individual dispersal, lake migration and resulting patterns of spatial resource partitioning and connectivity among populations. Our results revealed that out of five sampled sites, four groups showed significant and temporally stable genetic differences: Chalifour, Takwa, Rupert, and 'Perch–Icon', the latter comprising walleye that reproduce in two geographically proximate tributaries of Mistassini Lake. Moreover, exclusion tests performed on both spawning fish and mixed stock samples indicated that all major populations were sampled, with only 1% of captured fish being of unknown origin. These observations confirmed that Mistassini Lake comprises four genetically distinct and temporally stable walleye populations.

A second objective was to investigate the relationships between individual biological characteristics (sex, size, age and population of origin), dispersal and lake migration. Overall, few walleye ($n = 61$, 7.6% of all fish collected on spawning grounds) could confidently be identified as dispersers. When reassigning spawning fish to the four baseline groups, misassigned individuals were generally absorbed (except for the Rupert population) by the geographically closest populations (see Castric & Bernatchez 2004 for similar examples in salmonids). We observed higher levels of dispersal between populations Takwa, Chalifour, and Perch–Icon than between Rupert and the three other populations. A larger influx of dispersers apparently moved in a North-South axis within the main lake while the Rupert population showed lower levels of exchanges with the three other populations (less than 2.5% of all spawning individuals per site). The investigation of the relationships between individual biological characteristics (sex, size, age and population of origin) and dispersal revealed that the population of origin of the dispersers was the only factor significantly explaining differential dispersal among individuals. This pattern was largely driven by the fact that Rupert population produced fewer dispersers compared to the other three populations. This corroborated the observed pattern of lake migration whereby walleye from the Rupert River population tended to remain in the vicinity of their spawning location, while the other three populations moved more extensively within the lake, especially walleye from the Takwa population, which migrated to the most southern part of the lake, some 150 km away from their river of origin (Fig. 5). The ANOVA, corroborated these observations by showing that fish originating from the Rupert population migrated over significantly shorter distances within the lake than walleye from the three other populations. Consequently, proportions of genetic admixture were congruent with this pattern of asymmetrical dispersal, which translated into higher levels of shared genetic admixture between populations Perch–Icon, Chalifour and Takwa, relative to the Rupert River population. Besides revealing the effect of population of origin in explaining differential pattern of lake migration, the ANCOVA showed that larger fish from each population tended to migrate further in the lake. This supported (Wolfert 1969)

observations of a tendency for older walleyes to move more extensively than younger fish.

### *Population structure and connectivity; comparisons with Mistassini Lake brook charr*

Our results provided evidence that asymmetrical and population-specific differential dispersal plays an important role in determining the level of genetic connectivity between walleye populations in Mistassini Lake. This may, in turn, theoretically influence the correlations between evolutionary trajectories of these subdivided populations (Whitlock 2001). However, this does not rule out the possibility that historical processes may also have contributed to the differential pattern of genetic connectivity we observed, particularly among the three inflows (Perch–Icon, Chalifour, Takwa) vs. the outflow (Rupert) populations. For instance, in a previous study of the brook charr *Salvelinus fontinalis* inhabiting Mistassini Lake, Fraser and Bernatchez (2005a, 2005b) provided evidence supporting the hypothesis that Mistassini Lake represents a secondary contact zone between ancestral populations of this species that evolved in allopatry. Interestingly, the overall pattern of genetic structuring observed for brook charr was analogous to that we observed for walleye. Thus, as we observed for walleye, brook charr reproducing in the Rupert River dispersed less and were genetically more distinct relative to the three brook charr populations reproducing in lake tributaries. Moreover, Fraser & Bernatchez (2005b) showed that outflow (Rupert) and inflow populations clustered distinctively with individuals originating from the James Bay and Lake Saint-Jean watersheds, respectively. This interpretation of distinct historical origin for brook charr from the Rupert population relative to others was supported by geological data (Bouchard 1980) demonstrating that isostatic movement following the last Pleistocene glaciation (7000–8000 BP) forced Mistassini Lake outflow to move from an initial southwest direction to its present location (Rupert river, flowing westward).

Similarly, there are lines of evidence supporting the hypothesis that walleye associated with the Rupert River may have originated from an ancestral group that was distinct from walleye that colonized Mistassini Lake tributaries. First, walleye from the Rupert River are genetically the most distinct and behaved differently than the other three populations. Moreover, in a pioneer phylogeographical study of mitochondrial DNA variations across the species range, Billington *et al*. (1992) observed 34 distinct haplotypes, three of them being very common and representing distinct evolutionary lineages. One of these common haplotypes, associated with the Missourian refugium, was found throughout populations sampled in northern Ontario as well as in the James Bay drainage, but not further to the East. A second common haplotype associated with the Mississippian glacial refugium was detected in more eastern populations sampled in central Québec and in the Saint Lawrence River system. Additionally, an area located west of Mistassini Lake is believed to be a secondary contact zone for fish originating from distinct glacial refugia in many species (Turgeon & Bernatchez 2001). Altogether, these observations make it plausible that as previously reported for brook charr, Mistassini Lake was colonized by two evolutionary lineages of walleye being associated with the Missourian and Mississippian refugia, respectively.

Similarities observed for population structure and connectivity between walleye and brook charr from Lake Mistassini are also noteworthy. Namely, these two species are usually considered as very distinct in terms of their life cycle and behaviour. Thus, brook charr is known as a sensitive species, intolerant to warm water, very selective regarding their reproductive habitat, and harbours complex mating behaviours (Power 1980; Morrison & Smith 1986). They also have a relatively short life expectancy (generally 4–6 years) and are known to travel and feed alone or in small schools (Fraser & Bernatchez 2005a). On the other hand, the walleye prefer warm waters, are very gregarious, can live up to 20 years old, and are not intensely selective in regard with their habitat (Scott & Crossman 1973; Hazel & Fortin 1986). They are also broadcast spawners and do not build nests. Nevertheless, both studies observed two major genetic groups within the lake: the Rupert population and the populations associated with the tributaries (the north rivers for brook char and Chalifour, Perch–Icon and Takwa for walleye in the present study). In both cases also, the amount of gene flow was noticeably higher between the tributaries than with the outflow population, even with the absence of physical barriers to dispersal. These similarities are best explained by historical contingencies paired with large-scale habitat structure constraining movements and restraining extensive exchanges between these groups.

### *Limited evidence for sex-biased dispersal in walleye*

Here, both methods used failed to significantly detect a potential bias between genders. Yet, the assignment index provided indications that behavioural divergence between populations might be present in the system, with an overall mean value revealing a tendency towards male-biased dispersal. Thus, when populations were analysed individually, Chalifour, Takwa and Rupert showed a propensity towards males' dispersal while Perch–Icon demonstrated the opposite trend (Table 7). A few factors could be responsible for the fact that sex biased dispersal, if present, was not clearly perceived within Mistassini Lake walleye. First, genetic methods such as the creation of an assignment index are efficient only in situations where sex-bias is pronounced (Goudet *et al*. 2002). In an exhaustive analysis of available

genetic methods used to detect sex-biased dispersal, Goudet *et al*. (2002) concluded that there was little hope of detecting significant results when bias intensities were less than 80:20 (80% of dispersers of one sex and 20% of the other). Second, both female- and male-biased dispersal could potentially occur in the studied system, but at variable degrees depending on the population. As a result, pooling samples in this study was unlikely to provide relevant informations concerning a putative bias between sexes, especially when the samples originating from the population demonstrating a trend towards female-biased dispersal (opposite from the overall trend) account for more than 40% of the pooled samples (270 out of 652 individuals). On the other hand, when populations were analysed individually, the reduction in the number of analysed individuals may have considerably reduced the power of detecting a significant signal of sex-biased dispersal (e.g. Hansen *et al*. 2001). Finally, except for males in population Perch–Icon ($0.009 \pm 0.103$) and females in population Chalifour ($0.210 \pm 0.331$), all population mean values were negative (six out of eight), suggesting that overall, both sexes exhibit a propensity for dispersal (Mossman & Waser 1999).

Previous attempts to detect dispersal bias between genders in walleye showed contradictory results. In a study comparing patterns of allozyme and mtDNA variation, McParland *et al*. (1999) observed a trend towards female-biased dispersal, although this result was not statistically supported. Stepien & Faber (1998) looked at mtDNA control region sequences, which showed no difference in the distribution of haplotypes between males and females in any of the sampled spawning sites. These results combined with ours tend to corroborate Clarke's *et al*. (1997) who concluded in a review of sex-biased dispersal in birds that 'the existing literature already strongly suggests that for many species it may be inappropriate to consider a sex bias in dispersal to be a species constant'. These observations are concordant with results of sex-bias determination in brook charr *Salvelinus fontinalis* inhabiting Mistassini Lake (Fraser *et al*. 2004). These authors revealed that northeast rivers spawning populations were skewed towards male dispersal while Rupert River spawning fish exhibited female-biased dispersal. Corrected assignment index built for 11 white-footed mice *Peromyscus leucopus* populations also revealed ambivalent results; eight populations showed a trend towards male-biased dispersal while three populations revealed reverse tendency (Mossman & Waser 1999). Pooled result confirmed that dispersal was skewed towards males in this species. Similarly, Dallimer *et al*. (2002) found that seven out of eight populations of red-billed quelea *Quelea quelea* were male biased while one was female biased, with pooled samples analysis showing male-biased dispersal. These analyses along with ours indicate that the scale (e.g. over the scale of many populations vs. that of a single population) at which behaviours are documented may impact on the conclusions being reached for a given data set. Thus, sex-biased dispersal is more likely to occur in reaction to local factors such as density and competition (Coulon *et al*. 2006), than resulting from specific mating behaviours (Greenwood 1980), which should induce similar observations across a whole species range.

### *Spatial and resource partitioning*

The occurrence of four genetically distinct and temporally stable walleye populations, which remain partially isolated in sympatry in the presence of continuous gene flow, suggest that divergent selection may play a role in maintaining the observed structure (Lu & Bernatchez 1999; Schluter 2001). Namely, there is increasing evidence indicating that spatial (rather than trophic) resource partitioning could play a substantial role in the maintenance of genetically distinct fish populations within a same lake (Taylor *et al*. 1997; Turgeon *et al*. 1999; Potvin & Bernatchez 2001; Fraser & Bernatchez 2005a). Many ecological and environmental factors may be responsible for spatial segregation of populations within a large lake, thus affecting their genetic structure and evolutionary pathway (Bijlsma & Loeschcke 2005). Fraser & Bernatchez (2005a) showed that outflow and inflow brook charr *Salvelinus fontinalis* populations used distinct lake habitats within Mistassini Lake, with the outflow population being associated with boulder beaches and inflow populations with dolomite cliff coastlines. In a study aiming at deciphering population structure and spatial partitioning of landlocked Atlantic salmon from Lac-St-Jean (Central Québec, Canada), Potvin & Bernatchez (2001) observed a temporally stable heterogeneous spatial distribution of four genetically distinct populations over a period of 25 years. Both studies on charr and salmon also revealed a negative correlation between spatial niche overlap and the extent of genetic differentiation between the populations. As proposed by Potvin & Bernatchez (2001), a possible determinism for such a correlation is that 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. 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. 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.

Habitat heterogeneity and environmental stresses might also play a significant role in explaining the differential pattern of spatial partitioning observed for walleye within Mistassini Lake. Located at the northern margin of walleye

distribution range, Mistassini Lake is characterized by relatively harsh thermal conditions for this species, which usually prefers summer temperatures ranging from 13 °C to 21 °C (Bernatchez & Giroux 2000). The large open water areas of the lake (North and South sectors, Fig. 5) are mostly composed of deep waters that remain cold all summer long. A sampling campaign held by Québec government officers from mid-August to September 1961 in the deep sections of the lake revealed that surface temperature never exceeded 15 °C and was generally lower. In addition, air temperature data (degree-days per year) gathered by Québec's ministry of natural resources over the last 30 years show that Mistassini Lake is included into two climatic zones. The north end of the lake is associated with a zone defined by 816–979 degree-days, while the south end is included in the 979–1141 degree-days area. With a length of 150 km in a southwest-northeast axis, Mistassini Lake is therefore most likely affected by a clinal variation in temperatures. Thermal constraints to walleye distribution in the lake were also reflected by anglers' catches, which were almost exclusively distributed in long and shallow back bays providing thermal refuge within the large open water sectors. In contrast, captures in the two other sectors (mouth of the Rupert and Baie-du-Poste) were not constrained to backwaters, these areas being characterized by warmer and shallower waters (Dupont, personal observations). Thus, walleye from the Takwa population must most likely move extensively across the large open water areas in search for suitable habitats while walleye belonging to the other populations Perch–Icon, Chalifour and Rupert may access thermally suitable feeding grounds close to their spawning sites. This thermal hypothesis would support the observed patterns of spatial distribution where walleye from the Takwa population were widely distributed throughout the large open water sectors while fish originating from the three other populations are mostly found close to their respective spawning sites. Other studies conducted in fish also revealed the potential influence of selection associated with differential thermal regimes on both genetic and phenotypic traits. In a study examining the effect of selected lake parameters on genetic diversity for 46 walleye populations (Ontario, Canada), Cena *et al*. (2006) showed that genetic diversity was positively correlated with the amount of growing degree-days, which led the authors to suggest that low temperatures may be a stressful parameter influencing genetic diversity, often correlated to effective population size. Additionally, Koskinen *et al*. (2002) demonstrated, in a common garden experiment, that offspring originating from different grayling populations *Thymallus thymallus*, separated since only 11.8–22.0 generations, performed best in rearing temperatures corresponding to their natural conditions. This supports the hypothesis that selection acted in favour of local adaptations in relation with thermal regimes in a relatively short timeframe. Therefore, we propose that, along with the history of colonization of the lake, the gradient of habitat availability combined with differential selective regimes imposed by environmental stresses may account for the observed pattern of stable spatial partitioning among Mistassini Lake walleye populations, which in turn contribute to reducing gene flow between spawning aggregations. In conclusion, this study underlined the relevance of using individual-based assignment methods in order to decipher the dynamics of wild populations, especially regarding the role of behavioural mechanisms involved in spatial partitioning and differential dispersal, and that may be responsible for the maintenance of genetic structure among sympatric populations.

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This research is part of Pierre-Philippe Dupont's M.Sc. thesis, which aims at studying the roles of evolutionary, environmental and behavioural factors on the genetic structuring patterns of northern Walleye (*Sander vitreus*) populations. PPD is currently project manager in environment for GENIVAR, a Canadian leader in consulting engineering. Vincent Bourret was an undergraduate student involved in this study, and he is currently studying the impacts of metal contamination on population genetics. Louis Bernatchez supervised PPD's M.Sc. thesis. LB's interests relate to the understanding of patterns and processes of molecular and organismal evolution, and their relevance to conservation.

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