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The landscape genetics of yellow perch (*Perca flavescens*) in a large fluvial ecosystem

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Abstract

Landscape genetics is being increasingly applied to elucidate the role of environmental features on the population structure of terrestrial organisms. However, the potential of this framework has been little explored in aquatic ecosystems such as large rivers. Here, we used a landscape genetics approach in order to (i) document the population structure of the yellow perch (*Perca flavescens*) by means of genetic variation at microsatellite markers, (ii) assess to what extent the structure was explained by landscape heterogeneity, and (iii) interpret the relevance of interactions between genetics and landscape for management and conservation. Analysis of the genetic variation among 1715 individuals from 16 localities and distributed over 310 km in the freshwater section of the Saint Lawrence River (Québec, Canada) revealed a relatively modest level of genetic structuring (F_{ST} = 0.039). Application of the Monmonier's algorithm combining geographical and genetic information identified three zones of restricted gene flow defining four distinct populations. Physical barriers played a more important role on gene flow and genetic structure than waterway geographical distance. We found correlations between genetic differentiation and presence of distinct water masses in the sector of Lake Saint-Louis (r = 0.7177, P = 0.0340) and with fragmentation of spawning habitats in the sector of Lake Saint-Pierre (r = 0.8578, P = 0.0095). Our results support the treatment of four distinct biological units, which is in contrast with the current basis for yellow perch management. Finally, this study showed that landscape genetics is a powerful means to identify environmental barriers to gene flow causing genetic discontinuities in apparently highly connected aquatic landscapes.

Keywords: conservation, fish, isolation-by-distance, landscape genetics, microsatellite DNA, population structure

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Introduction

Natural populations occur in a landscape mosaic in which environmental features restrict or promote movements of individuals and genes (Taylor *et al*. 1993; Sork *et al*. 1999). Pattern of gene flow may have a profound influence on evolutionary trajectories of populations as well as on their spatial organization and persistence in time and space (Wiens 1997). Consequently, the importance of understanding how landscape features may affect the extent of genetic connectivity among populations has long been recognized (e.g. Wallace 1860; Fisher & Ford 1947; Crisci 2001). Yet, it is only recently that the study of interactions between environmental features and patterns of population genetic structure has been formalized as a discipline, namely landscape genetics (Manel *et al*. 2003). This framework applies methods developed in landscape ecology (reviewed in Storfer *et al*. 2007) in order to document the spatial pattern of genetic variation, and provide insights about environmental factors that may influence gene flow among populations (Piertney *et al*. 1998; Keyghobadi *et al*. 1999; Castric *et al*. 2001; Funk *et al*. 2005; Guillot *et al*. 2005). This, in turn, may provide important clues about the dynamics

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of populations in relation with landscape features, which may be relevant for improving conservation and management practices, and better evaluate the potential impacts of landscape disturbance on species long-term persistence (e.g. Watts *et al*. 2004; Banks *et al*. 2005).

A number of recent studies highlighted the effects of landscape characteristics on patterns of genetic population structuring, including in birds (Piertney *et al*. 1998), insects (Keyghobadi *et al*. 1999), amphibians (Funk *et al*. 2005), plants (Bond *et al*. 2005; Kitamoto *et al*. 2005), mammals (Schwartz *et al*. 2003; Cushman *et al*. 2006), and fish (e.g. Angers *et al*. 1999, see below also). However, the importance of the physical nature of environments on population structure was already emphasized nearly 15 years ago by Ward *et al*. (1994), who summarized evidence showing that the average degree of genetic population structuring was more similar between mammals, reptiles and freshwater fishes than between birds and marine fishes. Namely, these authors suggested the patchwork nature of freshwater and terrestrial habitats, comparatively to the larger and more continuous nature of the marine and aerial environments offering more zones of impenetrable habitat, and thus, barriers to gene flow resulting in a more pronounced population subdivision (Ward *et al*. 1994). More specifically in fishes, Ward *et al*. (1994) demonstrated that freshwater species tend to display higher levels of genetic structuring than those inhabiting marine environments, with estuarine species found in an intermediate position. This generalization was mostly attributed to the fact that adults or larvae dispersal for freshwater species is more restricted than in marine environment because of the presence of unconnected or unsuitable habitats between drainages. More recently, several studies revealed significant genetic structuring in marine fishes explained by the presence of ecological or hydrographical barriers to dispersal, such as ocean currents or habitat discontinuity (Riginos & Nachman 2001; Knutsen *et al*. 2003; Jørgensen *et al*. 2005; Ruzzante *et al*. 2006). These observations highlight the fact that environmental barriers to gene flow causing genetic discontinuities can be found even in apparently highly connected landscapes such as marine environments. Such studies also illustrated the usefulness of conducting landscape genetics studies to better understand impacts of various landscapes on patterns of population structure and connectivity.

Large rivers of the world constitute a distinctive class of freshwater environments, namely for the connection they offer between the freshwater and marine realms, and for their important role to drain the world's freshwater reserves (CSL 1996). Moreover, large rivers are often characterized by fluvial lakes or isolated regions with shallower depths, less turbulence and longer retention times, interspaced with zones of highly dynamic river flow regimes, often incorporating inflows with distinct abiotic and biotic characteristics (Avise & Felley 1979; CSL 1996; Vincent & Dodson 1999; Frenette *et al*. 2003). Many large rivers have also been extensively altered by humans (Avise & Felley 1979). Such environmental complexity has hampered our understanding of fish population structure in large river systems compared to other aquatic habitats, such as lakes and streams.

In this study, we applied the landscape genetic framework to document the role of various environmental features on pattern of population structure in yellow perch (*Perca flavescens*) of the Saint Lawrence River, Quebec. The Saint Lawrence River is the largest river draining on eastern coastline of North America with a drainage surface of 1 610 000 km^2 and a length of 3260 km extending from the Great Lakes to the Gulf of Saint Lawrence. It also drains more than 25% of the world's freshwater reserves (CSL 1996; Vincent & Dodson 1999). Yellow perch is an abundant freshwater fish largely distributed throughout northeastern North America from Florida, USA to the southern James Bay. It is also highly exploited both commercially and by angling (Thorpe 1977; Todd & Hatcher 1993). During the spawning season (late April to early May), which coincides with the spring flood in the Saint Lawrence River, yellow perch uses flood plains as spawning grounds corresponding to shallow areas with dense vegetation and slight water currents, found mainly in the lake peripheries or around various small islands met on the course of the river. Yellow perch generally move to feeding sites soon after spawning and to deeper areas in wintertime (Thorpe 1977; Craig 1987). Mark–recapture studies in the Saint Lawrence River have shown that yellow perch exhibit different dispersal behaviour that varies in space and time (Dumont 1996; de Lafontaine *et al*. 2002). Namely, despite the fact that yellow perch or closely related Eurasian perch (*Perca fluviatilis*) are generally considered sedentary (Fortin & Magnin 1972; Aalto & Newsome 1989; Järv 2000), long-distance dispersal (up to 175 km) has been reported for both (Böhling & Lehtonen 1984; Järv 2000; Miller 2003), and specifically for yellow perch in the Saint Lawrence River (Dumont 1996; de Lafontaine *et al*. 2002). On the other hand, zones of high water velocity may constitute barriers to gene flow for this species, which is rarely found in where current speed exceeds 45–60 cm/s (Fortin & Magnin 1972; Thorpe 1977; Craig 1987; CSL 1996). The population structure of yellow perch has been investigated by means of various genetic markers (Leary & Booke 1982; Strittholt *et al*. 1988; Billington 1993; Miller 2003). Yet, little attention has been paid to the impact of landscape features on the extent of genetic differentiation in the species (but see Miller 2003). In this context, our specific objectives were (i) to document the population structure of the yellow perch in the Saint Lawrence River by means of genetic variation at microsatellite markers; (ii) to assess to what extent the observed structure could be explained by landscape heterogeneity; and (iii) to interpret

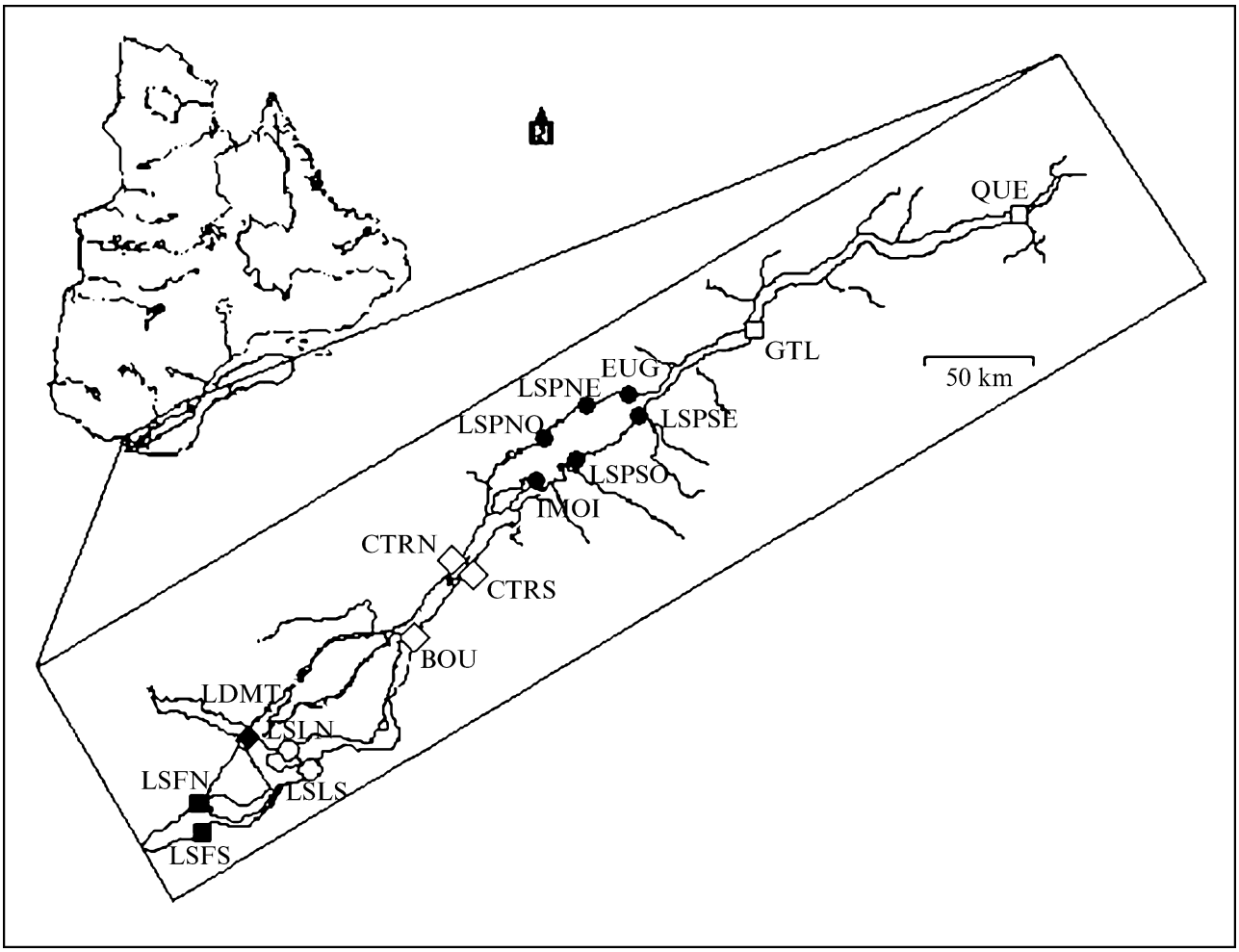

Fig. 1 Sampling locations of yellow perch in the Saint Lawrence River. Location names and abbreviations are given in Table 1. Symbols were used to indicate the lake or fluvial sections where the samples were collected. From west to east, dark squares, Lake Saint-François; black diamonds, Lake des Deux-Montagnes; white circles, Lake Saint-Louis; white diamonds, fluvial section from Boucherville to Contrecoeur; black circles, Lake Saint-Pierre; white squares, fluvial section from Gentilly to Quebec City.

the relevance of our findings for the management and conservation of yellow perch.

Materials and methods

Landscape features

The Saint Lawrence River is characterized by a heterogeneous natural landscape and by important anthropogenic alterations, especially to avoid excessive spring flooding (discharge regulation), and to enhance navigation (large artificial channel and frequent dredging) and hydropower (dams). From the eastern end of the Lake Ontario, its freshwater part begins with a nontidal fluvial section of 400 km, which crosses three large fluvial lakes with water flow dynamics characteristic of a river (Lake Saint-François, Lake Saint-Louis and Lake Saint-Pierre) (CSL 1996; Laviolette 2004; Fig. 1). The main channel of the Saint Lawrence River is dredged and relatively deep (the minimum warranted depth is 11.3 m) and fast flowing (about 0.5–2 m/s), whereas the shorelines of the fluvial lakes are shallow (< 4 m) and slower flowing (< 0.5 m/s) with extensive macrophyte beds (CSL 1996; Basu & Kalff 2000). In the fluvial section, the Saint Lawrence receives flow of several rivers characterized by distinct water masses. The 'green waters' flowing from the upper Saint Lawrence River and arriving through the Lake Saint-François form a water mass that converges with the 'brown waters' from the Ottawa River through Lake des Deux Montagnes and Rivière des Prairies (main discharge), Rivière des Mille-îles, and also into the Lake Saint-Louis (CSL 1996; Morin & Bouchard 2000). These two important

water masses differ by their physico-chemical composition, such as nutritive elements and dissolved oxygen concentrations (CSL 1996; Basu & Kalff 2000). A well-defined gyre of the green and brown water masses in the western part of the Lake Saint-Louis forms a third water mass or 'mixed waters' (Dumont 1996). In the main channel, the water masses flow in parallel a long way downstream and join with tributaries along the shorelines (CSL 1996). The Lake Saint-Pierre is the most important section of the freshwater part of the Saint Lawrence River in terms of wetland habitat surface (Frenette *et al*. 2003). There, during the spring flood, availability of yellow perch spawning habitats is increased by over 40% (Morin & Côté 2003). At the southwest entrance of the lake, many islands form an archipelago, which offer additional spawning habitats for yellow perch (Mingelbier *et al*. 2004). Many other spawning grounds are found outside of the Lake Saint-Pierre on the shorelines, especially into other fluvial lakes. However, spawning habitats are almost inexistent into fluvial corridors such as between Contrecoeur and Lake Saint-Pierre, except around the small islands of Boucherville and Contrecoeur. The freshwater part is also impacted by anthropogenic alterations, such as the natural end of the Lake Saint-François, where dams were constructed, which created a barrier to fish dispersal (Dumont 1996). At the entrance of the Lake Saint-Pierre, there are also five small dams, which were constructed during the 1930s to direct water flow into the principal canalization and increase water levels upstream for navigation (Morin & Côté 2003). The freshwater section of the Saint Lawrence River is followed downstream by a fluvial estuary of 160 km in length, which is characterized by highly dynamic hydrological conditions due to important semidiurnal tidal amplitudes (4.1–5.8 m), as well as strong water mixing (Leclerc & Desgranges 2005). The end of this freshwater tidal section is associated with a maximum turbidity zone (MTZ) with high residence times downstream of Quebec City (turbidity: 50 to > 20 mg/L), where highly productive planktonic and larval fish communities are retained by flood tides (Dodson *et al*. 1989; Laprise & Dodson 1989).

Sample collection

Yellow perch adults were collected on spawning grounds during 2003 and 2004 (April–May) between the Lake Saint-Francois and Gentilly (Fig. 1). With a few exceptions (Table 1), the same localities were sampled in 2003 and 2004 for assessing the temporal stability of population structure. The mean number of individuals per sample was 60, comprising 30 adult females and 30 adult males. In addition, yellow perch from Saint Nicolas, near Quebec City, were collected during the end of the spring and autumn to test whether dispersal from the upstream section revealed by a mark–recapture study (de Lafontaine *et al*. 2002) translated in weak genetic differentiation of these downstream fish. Fish were obtained from commercial fishermen from all localities, except for Saint Nicolas, where there was an experimental trap fishery. A total of 1018 and 697 individuals were collected for 2003 and 2004, respectively (Table 1). Fin tissues were stored in 95% ethanol.

DNA extraction and microsatellite analyses

DNA was extracted using standard DNeasy Tissue Kit and Millipore (QIAGEN) following the manufacturer's instructions. Polymerase chain reaction (PCR) amplification and genotyping were conducted for 10 dinucleotide microsatellite loci (*PflaL1*, *PflaL3*, *PflaL4*, *PflaL5*, *PflaL6*, *SviL10*, *Svi17*, *Svi5*, *Cv09* and *E06*) chosen for their capacity to detect polymorphism among all primers developed, respectively, for yellow perch (*Perca flavescens*), walleye (*Stizostedion vitreum*), striped darter (*Etheostoma virgatum*) and tessellated darter (*Etheostoma olmstedi*) (Borer *et al*. 1999; Wirth *et al*. 1999; DeWoody 2000; Leclerc *et al*. 2000; Eldridge *et al*. 2002; Porter 2002). Because we observed stutters and nonamplifying alleles for the loci *PflaL4* and *Cv09*, respectively, eight loci were finally used. Microsatellite markers were amplified separately with PCR in 12-μL reaction volumes composed of ddH_2O, 1.0 μL 10× reaction buffer (10 mM Tris-HCl, 1.5 mM $MgCl_2$, 0.1% TritonX-100, 50 mM KCl), 50 ng of template DNA, 0.3 μL dNTPs (10 mM each dNTPs), 0.83 μM fluorescently labelled (forward) primer, 0.45 μM of reverse primer, and 1.0 U *Taq* DNA polymerase. The PCR programme used was 95 °C for 5 min; 35 cycles at 95 °C for 30 s, 45 s at a marker-specific annealing temperature (Table 2) and 45 s at 72 °C; and a final 10 min at 72 °C. Amplified products were resolved on an ABI PRISM 3100 genetic analyser (Applied Biosystems Inc.) using GeneScan 500 ROX as a size standard and scored using GENESCAN 3.7 and GENOTYPER 3.7 software (Applied Biosystems Inc.).

Genetic data analyses

Genetic diversity within each sample was quantified for each locus in terms of observed and expected heterozygosities (H_O and H_E), number of alleles per locus (A) using GENETIX 4.02 (Belkhir *et al*. 2001), as well as for allelic richness ($\hat{A}$) using FSTAT 2.9.3 (Goudet 2001). Allelic richness was calculated for the smaller sample size ($n = 40$) (Leberg 2002). We also tested for conformity to Hardy–Weinberg expectations of genotypic frequencies for each locus and across all loci, and for linkage disequilibrium between all loci pairs using GENEPOP 3.3 (Raymond & Rousset 1995b). When applicable, the sequential Bonferroni procedure was used to maintain type I probability error at $\alpha = 0.05$ ($p_{adj} = \alpha/k_i$; Rice 1989). All other statistical tests

Table 1 Samples of yellow perch from the Saint Lawrence River used in the present study

	Sample	Region	Sampling time	Code	Sample size
1	Quebec City		Jun 2003	QUE(P03)	57
			Jun 2004	QUE(P04)	17
			Sep 2003	QUE(A03)	110
			Sep 2004	QUE(A04)	16
2	Gentilly		May 2003	GTL(03)	60
			May 2004	GTL(04)	77
3	Saint-Eugène		May 2004	EUG(04)	60
4	Lake Saint-Pierre	Northeast	May 2003	LSPNE(03)	60
		Northeast	May 2004	LSPNE(04)	62
		Southeast	May 2003	LSPSE(03)	60
		Southeast	May 2004	LSPSE(04)	60
		Northwest	May 2003	LSPNO(03)	60
		Northwest	May 2004	LSPNO(04)	70
		Southwest	May 2003	LSPSO(03)	60
		Southwest	May 2004	LSPSO(04)	62
5	Île du Moine		May 2003	IMOI(03)	60
6	Contrecoeur	North	May 2003	CTRN(03)	60
		North	May 2004	CTRN(04)	60
		South	May 2003	CTRS(03)	60
		South	May 2004	CTRS(04)	60
7	Boucherville		May 2003	BOU(03)	43
8	Lake Saint-Louis	North	May 2003	LSLN(03)	60
		South	May 2003	LSLS(03)	83
		South	May 2004	LSLS(04)	50
9	Lake D. Montagnes		May 2003	LDMT(03)	65
			May 2004	LDMT(04)	49
10	Lake Saint-François	North	May 2003	LSFN(03)	60
		South	May 2003	LSFS(03)	60
		South	May 2004	LSFS(04)	55

Table 2 Microsatellite loci characteristics. Number of alleles per locus (*N*) and PCR annealing temperature (T_a) in Celcius degree are provided. Accession numbers were not available for Svi 17 and E06

	Locus	Repeat motif	Primer sequence (5′–3′)	Size range (bp)	*N*	T_a (°C)	Accession no.
1	*PflaL1*	$(GA)_{27}$	AAGCAGCCTGATTATATATC CAGACAATTAAACATGCAAC	94–130	11	50	AF211826
2	*PflaL3*	$(TG)_{18}$	GCCGAATGTGATTGAATG CGCTAAAGCCAACTTAATG	128–194	21	53	AF211828
3	*PflaL5*	$(GT)_{27}$	TGAGAGCCCATGAATTAC GCAAACACAGCCAATTTAG	126–156	13	53	AF211830
4	*PflaL6*	$(TG)_{18}$	GCATACATATAAGTAGAGCC CAGGGTCTTCACTATACTGG	136–180	17	53	AF211831
5	*Svi17*	$(AC)_{13}$	GCGCACTCTCGCATAGGCCCTG CGTTAAAGTCCTTGGAAACC	150–190	10	52	G36963
6	*Svi5*	$(AC)_{18}$	CTTAATTCCCCCAGCAAC TGTGTGCATCATTATCACTG	156–204	15	52	----------
7	*SviL10*	$(CA)_{33}$	GGTAATGTATTTTCAGTTATTGC GCTGTTCTCCAAGTAAAGCC	196–278	26	51	AF144743
8	*E06*	$(AC)_n$	AACAGATGATGCTCAGTGG ATCGACGACATACGAGTTCTG	106–164	14	57	----------

were at the 0.05 level unless stated otherwise. The method of Raymond & Rousset (1995a) in GENEPOP 3.3 (Raymond & Rousset 1995b) was used to detect global differentiation on allelic frequencies between sampling sites. To estimate the extent of genetic differentiation between study sites, global and pairwise measures of genetic differentiation based on allelic identity were calculated (*F*-statistics, e.g. θ; Weir & Cockerham 1984) using GENETIX 4.02 (Belkhir *et al*. 2001). We then used the allele size randomization test of Hardy *et al*. (2003) to assess the relative importance of drift (θ) vs. mutation (*R*-statistics, e.g. R_{ST}; Michalakis & Excoffier 1996) for population differentiation with 1000 permutations of allele sizes using SPAGEDI 1.1 (Hardy & Vekemans 2002). When the null hypothesis of $F_{ST} = R_{ST}$ was rejected ($\alpha = 0.05$), R_{ST} measures were considered to better reflect the genetic differentiation between study sites, because of the contribution of stepwise-mutation model (SSM)-like mutations in the genetic differentiation.

The maximum difference Monmonier's algorithm of Manni *et al*. (2004) implemented in the program BARRIER 2.2 was used to identify the geographical areas associated with genetic discontinuities in the system. Briefly, the Monmonier's algorithm allows identifying boundaries associated with the highest rate of genetic change on a map where the samples are represented according to their geographical coordinates and are connected by Delaunay triangulation with edges associated to genetic differentiation measures (θ; Weir & Cockerham 1984). Analyses were conducted both for each of the eight loci separately and for the complete data set. The analysis of individual loci allowed to determine how many loci supported each identified barrier, and thus to verify the extent of redundancy of the data. Only barriers supported by at least half of the loci were retained. Because each barrier is formed of different edges separating the samples, we mentioned for each barrier the number of loci that supported completely the barrier and those which supported partially the barrier (only some edges of the barrier). A distance matrix based on the full data set was employed in BARRIER 2.2 to build a map of 'consensus barriers'. All these analyses were conducted for both sampling years to verify the temporal stability of the resulting barriers. The analyses were performed again with samples from 2003 but this time with the exclusion of corresponding missing samples from 2004 to verify if some barriers observed in 2004 resulted from different sampling regime. Graphical plotting of population differentiation was also generated by a principal component analysis (PCA) of allelic frequencies using PCA-GEN 1.2.1, with significance of each principal component assessed with 10 000 randomizations of genotypes (Goudet 1999).

A hierarchical AMOVA was performed using ARLEQUIN 2.0 (Schneider *et al*. 2000) by first grouping study sites by year of sampling (2003 and 2004). This analysis was conducted to assess the temporal stability of the genetic diversity, and the validity of grouping temporal samples. A second AMOVA was conducted for estimating the proportion of genetic variance distributed among spawning groups identified by BARRIER 2.2. Finally, a third AMOVA was run on groups defined on the basis of six lake or fluvial sections where samples were collected and corresponding to the current basis for yellow perch management. From West to East these were Lake Saint-François, Lake des Deux Montagnes, Lake Saint-Louis, the fluvial section from Boucherville to Contrecoeur, Lake Saint-Pierre, and the fluvial section from Gentilly to Quebec City. This allowed comparing the extent of genetic variance explained by groups defined either by BARRIER 2.2 and water masses.

Landscape genetic analyses

To test the possible influence of landscape on genetic discontinuities observed in the system (see results), information were collected for the following features: dams, water masses (CSL 1996; Morin & Côté 2003), mean values of turbidity and temperature of each sampling site (obtained from Désilets & Langlois 1989). Also, a map representing the estimated surface of 'good spawning habitats' for yellow perch from Boucherville to downstream of Lake Saint-Pierre was obtained from the Ministère des ressources naturelles, de la faune et des parcs du Québec (MRNFP) and the Service Météorologique of Canada (Mingelbier *et al*. 2004). This map was constructed on the basis of variables representing three important criteria in the selection of spawning grounds by yellow perch: vegetation surface, water depth and current velocity, and was built according to a scenario of water flow between 9500 and 14 500 m^3/s, which represents the mean range of water flow in the Saint Lawrence River (CSL 1996; Mingelbier *et al*. 2004; Fig. 2).

Information about each landscape feature was transformed into a measure of ecological distance between sampling sites as follows: (i) A value of 1 or 2 was assigned to pairs of sampling sites separated by 1 or 2 physical barriers (dams) in the environmental distance matrix, and a value of 0 to pairs of populations not so separated, under the assumption that dams could restrict gene flow; (ii) The numbers of the main different water masses (from 0 to 3) to cross between each sampling location was indicated as ecological distance in the matrix. The presence of different water masses separating populations was simplified into integers because it was not possible to treat these data otherwise. Differences in mean values of (iii) turbidity and (iv) spring temperature between each pair of sampling sites were calculated. (v) Finally, using MAP INFO PROFESSIONAL 8.5 (MapInfo Corporation 2006, www.mapinfo.com), the shortest distances to cover without good spawning habitats for fish between each pair of sampling sites were measured on the map of good spawning habitats, which

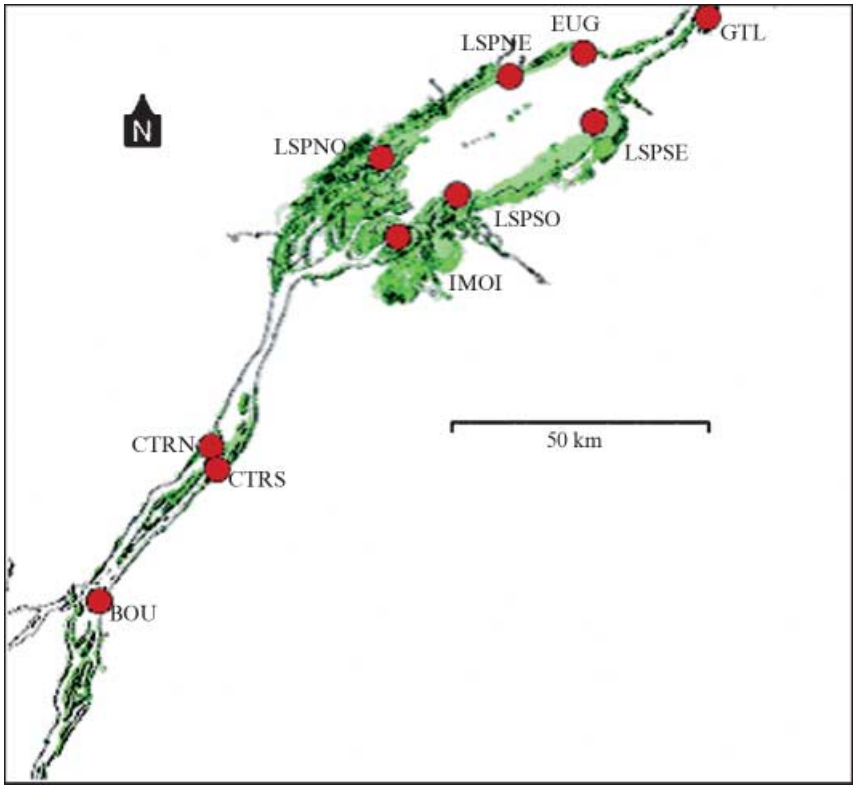

Fig. 2 Map showing estimated surface of 'good spawning habitats' for yellow perch from Boucherville to downstream Lake Saint-Pierre, obtained from the Ministère des ressources naturelles, de la faune et des parcs du Québec (MRNFP) and the Service Météorologique of Canada (Mingelbier *et al*. 2004). The map was built on the basis of three variables: vegetation surface, water depth and current force, with a scenario of water flow between 9500 and 14 500 m^3/s corresponding to the mean range of water flow in the Saint Lawrence River.

was available only for the river section area between Boucherville and the eastern part of Lake Saint-Pierre. Mantel tests (Mantel 1967) and partial Mantel tests (Legendre & Legendre 1998) were implemented in IBD web service of Jensen *et al*. (2005) (available at http://ibdws.sdsu.edu) to investigate the association between pairwise genetic distances (θ; Weir & Cockerham 1984), each of ecological distances described above, and shoreline geographical distances (all expressed as pairwise distances in matrix). For each test, 30 000 matrix randomizations were used. All distances were measured between centroids of sampling sites using MAP INFO PROFESSIONAL 8.5.

Finally, we used the hierarchical Bayesian method implemented in the software GESTE version 1 (Foll & Gaggiotti 2006) to corroborate the results of Mantel and partial Mantel tests conducted at large spatial scale regarding the potential influence of temperature, turbidity and water mass (and their interactions) in shaping the genetic structure of yellow perch. This method estimates F_{ST} values for each local population and relates them to environmental factors using a generalized linear model. Posterior probabilities associated with each factor, estimated from the number of times the algorithm visited each model, allowed the identification of factors most influencing genetic structure. We used a burn-in of 2000 iterations to attain convergence and a total chain length of 1×10^5 iterations. These parameters were sufficient to attain convergence and have also been shown to be adequate under different data set scenarios (Foll & Gaggiotti 2006). Each analysis was conducted for three replicates to ensure consistency of results.

Results

Descriptive statistics

All loci were moderately to highly polymorphic, with 10–26 alleles observed per locus, and allelic richness ranging from 2.89 in Lake Saint-Pierre southeast (LSPSE) 2003 (*PflaL5*) to 18.09 in Lake Saint-Pierre northeast (LSPNE) 2004 (*SviL10*) (Table S1, Supplementary material). This translated into average expected heterozygosity (H_E) ranging from 0.31 in Gentilly (GTL) 2003 (*PflaL5*) to 0.92 in Lake Saint-François north (LSFN) 2003 (*SviL10*), and overall mean values of allelic richness of 7.98 (mean values per locus ranging from 7.41 to 8.87) and expected H_E of 0.69 (mean values per locus ranging from 0.64 to 0.73). Hardy–Weinberg equilibrium in all loci and sites was not rejected in all but 3 out of 200 tests after Bonferroni correction ($\alpha = 0.002$, $k = 25$), with heterozygote deficiency detected in Lake Saint-Louis south (LSLS) 2003, LSLS 2004 and Lake D. Montagnes (LDMT) 2003 (*PflaL1*, *Svi5* and *E06*, respectively). Exact tests of genotypic linkage equilibrium revealed a lower proportion of significant adjusted *P* values than expected by chance (one of 60 comparisons).

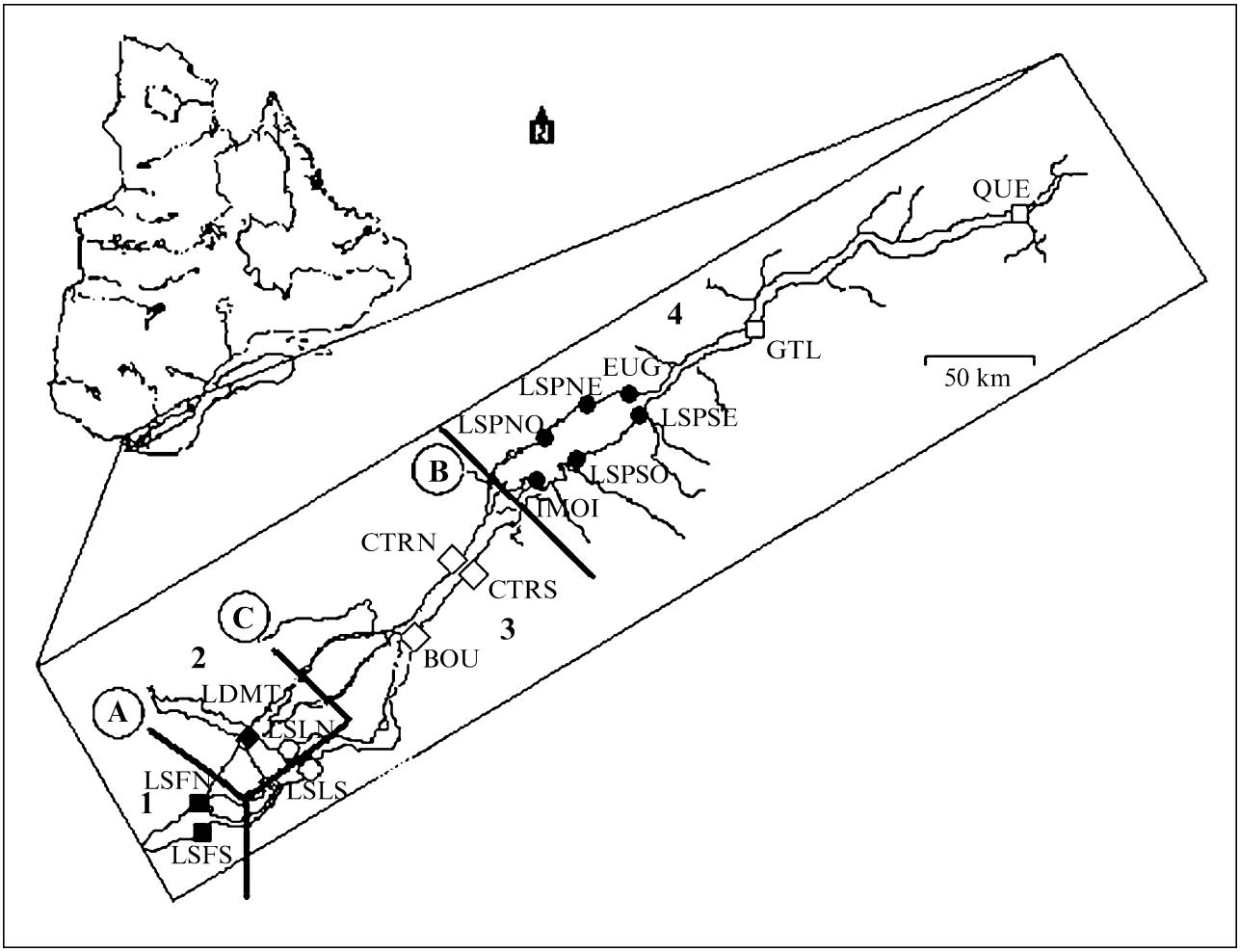

Fig. 3 Areas of genetic breaks as identified by BARRIER 2.2 using the Monmonier's algorithm (Manni *et al*. 2004). Samples were located according to the Delaunay triangulation. Barriers that were retained under the majority-rule criterion are identified by order of importance (A, B, and C). These barriers separate the system into four genetically distinct populations: 1) Lake Saint-François; 2) North of Lake Saint-Louis and Lake des Deux-Montagnes; 3) South of Lake Saint-Louis downstream to Contrecoeur; 4) and Lake Saint-Pierre downstream to Quebec City. See Fig. 1 for symbol definitions.

Population genetic structure

Global differentiation on allelic frequencies between sampling sites was first confirmed across all loci (χ^2 = infinite, d.d.l. = 16, $P < 0.001$). This translated into an overall relatively modest level of genetic differentiation across all sites of a global F_{ST} of 0.039 (Weir & Cockerham 1984). Pairwise θ values (*F*-statistics; Weir & Cockerham 1984) between sampling sites and probabilities showed that the extent of genetic differentiation between any pair of samples varied between 0 and 0.1107 (Table S2, Supplementary material). The global R_{ST} value was significantly higher than F_{ST} ($P < 0.001$), suggesting a role for historical separation on the global genetic differentiation in the system. However, only pairwise R_{ST} values for comparisons of sites implicating the northern or southern sectors of Lake Saint-François (LSFN or LSFS) were significant (R_{ST} ranging from 0.073 to 0.212, $0.0004 < P < 0.012$).

Analyses performed using BARRIER 2.2 identified three main genetic discontinuities (Fig. 3). The first break separated Lake Saint-François from all other samples and was supported completely by six loci and partially by the two other loci in 2003, and completely by five loci and partially by two more loci in 2004. The second break for 2003 separated Contrecoeur from locations further downstream with a complete support of five loci and a partial support of two more loci. This also corresponded to the third most important genetic discontinuity in 2004, which was supported completely by four loci and partially by two more loci. The third most important break for 2003 separated samples of Lake des Deux Montagnes (LDMT) and the northern part of Lake Saint-Louis (LSLN) from the southern

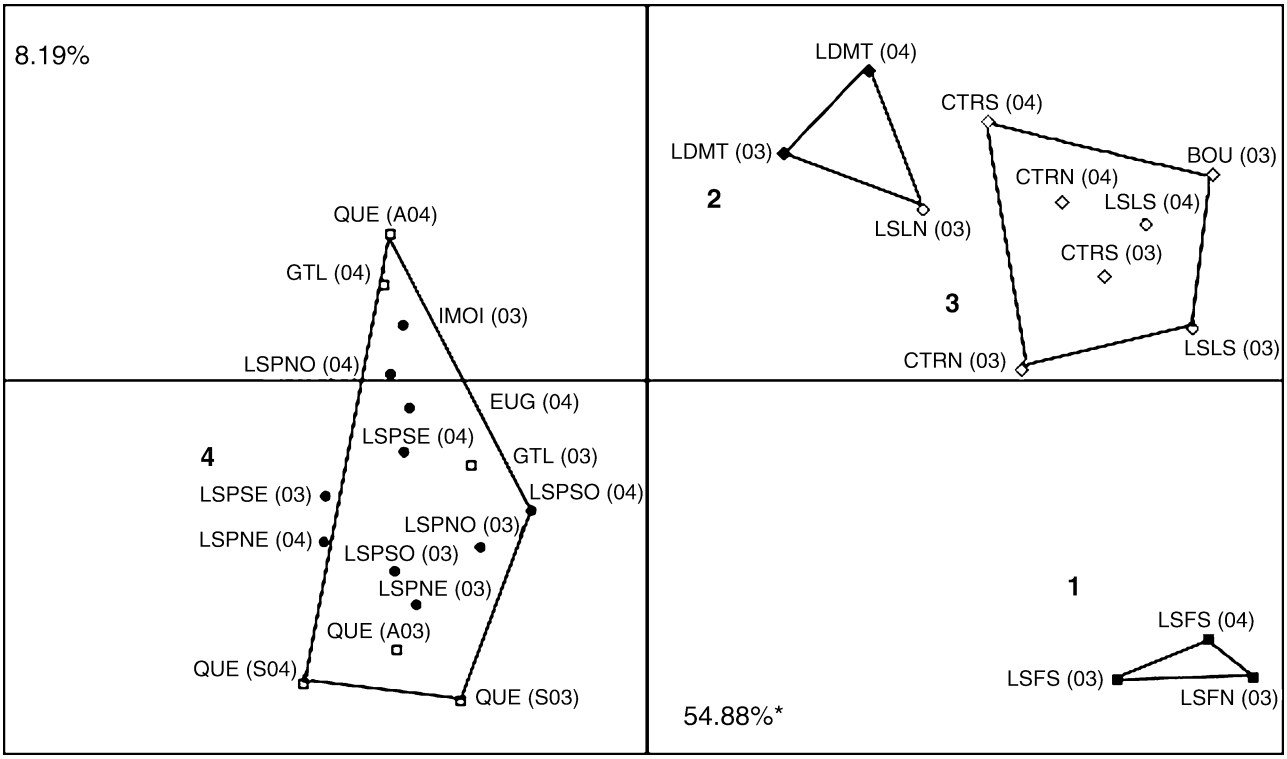

Fig. 4 PCA based on allelic frequencies by sampling sites using PCA-GEN 1.2.1 (Goudet 1999) with 10 000 permutations of genotypes. The first component explained 54.88% of variance ($P < 0.001$), and proportion of variance explained by the second component was not significant (8.19%, $P = 0.889$). The four groups previously defined with BARRIER 2.2 are delimited by lines. See Fig. 1 for symbol definitions.

part of Lake Saint-Louis (LSLS) and other samples downstream, which was totally supported by five loci. This break also corresponded to the second most important break in 2004. A fourth break not detected in 2003 was found in 2004, which separated the southern part of Lake Saint-Louis from other downstream samples. In eliminating the four samples from 2003 that were not collected in 2004, the exact same barriers observed for 2004 were obtained, including the additional fourth break, which was created by the missing sample of Boucherville immediately downstream of Lake Saint-Louis. This additional barrier was not retained in our results interpretation. Other genetic discontinuities identified by BARRIER 2.2 did not meet the majority-rule criterion of being supported by at least 50% of all loci, and therefore were not considered as significant.

Overall, the three geographical barriers that were significant and stable over the 2 years separated four genetically distinct populations of yellow perch: one population in Lake Saint-François, a second one extending from the northern part of Lake Saint-Louis to Lake des Deux-Montagnes, a third population extending from the southern part of Lake Saint-Louis downstream to Contrecoeur, and a fourth population including all samples from Lake Saint-Pierre and downstream to Quebec City. The PCA performed on allelic frequencies highlighted the occurrence of the same four genetically distinct populations revealed by BARRIER 2.2, which explained 63.07% of the variance on allelic frequencies, on the basis of the first dimension (54.88%, $P < 0.001$), and the second dimension (8.19%, $P = 0.889$) (Fig. 4).

The hierarchical analysis of molecular variance (AMOVA) did not allow to reject the null hypothesis of an absence of temporal variation in allelic frequencies between the two sampling years ($P = 0.545$; Table 3). Therefore, temporal samples were pooled for the two subsequent AMOVAS. These analyses revealed a significant proportion of explained genetic variance among groups, both for groupings resolved by BARRIER, as well as groupings based on lakes and fluvial sections. However, the proportion of explained variance by the former was about 20% higher (3.03% comparing to 2.41%, $P = 0.001$ in both cases; Table 3). The observed proportion of variance explained by differences among sites was marginal, representing less than 10% of the variance detected among the four major groups.

Landscape effects on patterns of population structure

There was a significant pattern of isolation by distance across the whole study area (Mantel test; $r = 0.527$, $P < 0.001$; Table 4). However, the presence of physical barriers (dams)

Table 3 Analysis of molecular variance (AMOVA) implemented in the ARLEQUIN 2.0 software (Schneider *et al.* 2000). Samples were partitioned according to (1) the year of sampling (2003 and 2004) to verify temporal stability; (2) the four genetically distinct populations defined by BARRIER 2.2; (3) the six lake and fluvial sectors found in the study area

	Groups compared	Number of groups	Components	Percentage of variation	*P* value
1	Temporal samples (2003 and 2004)	2	Among groups	0.08	0.5445
			Among sites	2.37	< 0.001
			Within sites	97.70	< 0.001
2	Genetically distinct populations	4	Among groups	3.03	< 0.001
			Among sites	0.40	< 0.001
			Within sites	96.57	< 0.001
3	Groups according to watersheds (lakes and fluvial sections)	6	Among groups	2.41	< 0.001
			Among sites	0.39	< 0.001
			Within sites	97.21	< 0.001

Table 4 Simple and partial Mantel tests showing the relationships between genetic distance (θ; Weir & Cockerham 1984), geographical distance, and environmental distances for physical barriers (dams), turbidity, water temperature, water masses and habitat fragmentation. Geographical distances were log-transformed before Mantel tests. Significant correlations (α = 0.05) are indicated (*)

	Region	Landscape feature	Mantel test/partial Mantel test	*r*	*P* value
1	All sites	Physical barriers	Genetics vs. log (geographical distance)	0.5265	< 0.001*
			Genetics vs. indicator	0.7671	< 0.001*
			Genetics vs. geo. distance, controlling indicator	0.1219	0.1580
			Genetics vs. indicator, controlling geo. distance	0.6626	< 0.001*
2	All sites	Turbidity	Genetics vs. log (geographical distance)	0.5265	< 0.001*
			Genetics vs. indicator	0.1928	0.0580
			Genetics vs. geo. distance, controlling indicator	0.4928	0.001*
			Genetics vs. indicator, controlling geo. distance	0.1067	0.1660
3	All sites	Water temperature	Genetics vs. log (geographical distance)	0.5265	< 0.001*
			Genetics vs. indicator	0.2098	0.0615
			Genetics vs. geo. distance, controlling indicator	0.4636	0.0146*
			Genetics vs. indicator, controlling geo. distance	0.1759	0.0661
4	All sites	Water masses	Genetics vs. log (geographical distance)	0.5265	< 0.001*
			Genetics vs. indicator	0.1922	0.0652
			Genetics vs. geo. distance, controlling indicator	0.4996	< 0.001*
			Genetics vs. indicator, controlling geo. distance	0.0084	0.4431
5	Lake des Deux Montagnes, Lake Saint-Louis, Boucherville, and Contrecoeur	Water masses	Genetics vs. log (geographical distance)	0.1032	0.3110
			Genetics vs. indicator	0.6963	0.0260*
			Genetics vs. geo. distance, controlling indicator	–0.2621	0.8542
			Genetics vs. indicator, controlling geo. distance	0.7177	0.0340*
6	Sectors from Boucherville to Gentilly	Spawning habitat fragmentation	Genetics vs. log (geographical distance)	0.6111	0.0031*
			Genetics vs. indicator	0.9119	0.0084*
			Genetics vs. geo. distance, controlling indicator	0.1305	0.2417
			Genetics vs. indicator, controlling geo. distance	0.8578	0.0095*

played a more important role than geographical distance on the overall pattern of genetic population structure (partial Mantel test excluding the effect of geographical distance; $r = 0.663$, $P < 0.001$). Correlation between genetic distances and the environmental distances for turbidity and water masses was nonsignificant ($r = 0.107$, $P = 0.166$; $r = 0.008$, $P = 0.443$, respectively), but nearly so for temperature ($r = 0.176$, $P = 0.066$). Genetic distances were also strongly correlated with the number of different water masses to cross between sampling locations. Namely, this was the case in a second partial Mantel test excluding the effect of geographical distance performed on samples collected in the sectors of Lake des Deux-Montagnes, Lake Saint-Louis, Boucherville and Contrecoeur ($r = 0.718$, $P = 0.034$). Moreover, the extent of genetic differentiation was strongly correlated with distance to cover without

Table 5 Posterior probabilities of the nine possible models explaining genetic differentiation of yellow perch populations as a function of (a) temperature and turbidity and (b) temperature and water mass. The temperature was the only significant factor selected by the Bayesian landscape genetic analysis in GESTE

a)

Model	Factors	Posterior probability
1	Constant	0.52
2	Temperature	0
3	Constant and Temperature	0.29
4	Turbidity	0
5	Constant and Turbidity	0.12
6	Temperature and Turbidity	0
7	Constant, Temperature and Turbidity	0.06
8	Temperature, Turbidity and interaction	0
9	All	0.01

b)

Model	Factors	Posterior probability
1	Constant	0.52
2	Temperature	0
3	Constant and Temperature	0.28
4	Water mass	0
5	Constant and Water mass	0.10
6	Temperature and Water mass	0
7	Constant, Temperature and Water mass	0.09
8	Temperature, Water mass and interaction	0
9	All	0.01

good spawning habitats for yellow perch between sampling locations located east of these sectors, that is from Boucherville up to Gentilly (partial Mantel test; $r = 0.858$, $P = 0.009$). This could not be tested further west as the map of good spawning habitats was not available.

Landscape genetic analyses implemented in GESTE revealed a potential influence of temperature in shaping the genetic structure of yellow perch at large scale, with a posterior probability of 0.29 (Table 5). All other factors and interaction between them were not retained by the Bayesian analysis (≤ 0.12 posterior probability). However, the mean σ^2 value associated with the temperature model was moderate: 0.26 ± 0.09. This parameter represents the deviation from the regression, and a low value is indicative of a good fit between the model and the F_{ST} values. The posterior probability for the null model was relatively high (0.52) which might suggest only a weak effect of temperature on the genetic differentiation of populations. Overall then, GESTE analyses did not provide further insights into the role of environmental features in shaping genetic structure in yellow perch.

Discussion

Geographical pattern of genetic variation in yellow perch

The first objective of this study was to document the genetic population structure of the yellow perch (*Perca flavescens*) in the Saint Lawrence River. Our analysis revealed a relatively modest level of genetic differentiation in the whole system. Yet, we identified three significant discontinuities into the geographical pattern of genetic variation, which defined four distinct populations: (i) Lake Saint-François, (ii) the northern part of Lake Saint-Louis and Lake des Deux Montagnes, (iii) the southern part of Lake Saint-Louis and the downstream fluvial section until Contrecoeur, and (iv) Lake Saint-Pierre downstream to Quebec City. Moreover, the same four distinct yellow perch populations were revealed by a PCA on the allelic frequencies by study sites.

The occurrence of four genetically distinct populations of yellow perch corroborates the results of previous studies on population dynamics and mark–recapture in the Saint Lawrence River. Thus, the genetic isolation of the Lake Saint-François population corroborates the observation of a single individual out of 2008 recaptured from the 20 530 tagged fish in Lake Saint-Louis and subsequently found in the Lake Saint-François (Dumont 1996). Also, Fortin (1970), Fortin & Magnin (1972) and Dumont (1996) all provided evidence for demographic independence between northern and southern populations of Lake Saint-Louis, associated with the sedentarity of these two populations. Thus, most recaptures of thousands of tagged yellow perch from Lake Saint-Louis were made within 10 km from tagging sites. Moreover, movements between the two areas were limited, with only 4% of recaptured yellow perch found in alternate

locations over a 3-year period (Dumont 1996). Differences in life-history traits between the two areas of Lake Saint-Louis further supported the existence of two distinct populations. Thus, yellow perch from the south shore are characterized by lower relative density, lower body condition and later sexual maturity compared to those from the north shore (Dumont 1996). Also, among the 140 yellow perch recaptured outside of the Lake Saint-Louis, 125 (90%) were recaptured into the Lake des Deux Montagnes (Dumont 1996, see also Pageau 1964). Our findings also corroborate previous observations about the existence of a distinct population in the Lake Saint-Pierre, and its partial isolation from populations upstream. For instance, the most important displacements recorded by Dumont (1996) were those of two yellow perch from the Lake Saint-Louis recaptured 105 km downstream at the entrance of Lake Saint-Pierre. Then, based on a mark–recapture study involving 10 000 tagged yellow perch, Leclerc (1985) reported extensive movements between north and south shores of Lake Saint-Pierre, which coincide with our observation of a single population within the lake. Leclerc (1985) also showed differential upstream vs. downstream dispersal behaviour of yellow perch from Lake Saint-Pierre. Concomitantly, de Lafontaine *et al*. (2002) provided evidence for seasonal movements of yellow perch between Lake Saint-Pierre and Quebec City located 176 km downstream. Downstream movements were more frequent during spring (May and June), just after the spawning season, whereas upstream movements occurred more in early fall (mid-September and October). These observations corroborate the genetic homogeneity and absence of significant population structuring among all samples collected between Lake Saint-Pierre and Quebec City. Together, previous tagging studies and our genetic survey highlighted striking differences in the scale of dispersal behaviour between yellow perch belonging to the Lake Saint-Pierre-Quebec City population and those further upstream in Lake Saint-Louis, where an almost complete lack of dispersal over a scale of 10 km and significant population structure was observed. Whether or not such difference in dispersal behaviour may be adaptive remains to be investigated in future studies. Alternatively, these differences could also be the result of landscape characteristics (see below).

Impacts of the heterogeneous large river landscape on the population subdivision

A second objective of this study was to document the role of landscape features in shaping the observed pattern of genetic population structure in yellow perch. To that aim, many factors were considered, including geographical distance per se, physical barriers (dams or waterfalls), water masses, turbidity, temperature, and distribution of spawning habitat. We first observed a significant pattern of isolation by distance in accordance with the fact that the dimension of the whole study area (almost 400 km) was larger than the longest dispersal distances reported for yellow perch (de Lafontaine *et al*. 2002; Miller 2003). However, the presence of physical barriers (dams) apparently played a more important role than waterway geographical distance in restricting gene flow among populations. The most important physical barriers, including dams but also natural waterfalls (CSL 1996) were found at the downstream end of Lake Saint-François, where we observed the most pronounced genetic discontinuity. Then, the existence of five small dams at the entrance of the Lake Saint-Pierre, before the archipelago (Morin & Côté 2003), was also associated to another putative barrier to gene flow. Since dams and waterfalls represent firm barriers to gene flow that remain stable over time, they represent the most likely landscape features to cause genetic isolation to develop over time. It is therefore logical that the two most important genetic discontinuities we identified were associated with physical barriers.

Correlations between genetic and the environmental distances for turbidity and water masses were nonsignificant in all cases when considering the whole study area. The correlation between genetic distances and differences in temperature between sites was low, but almost significant ($r = 0.1759$, $P = 0.0661$). Interestingly, temperature was also the only factor retained by the Bayesian landscape genetic analyses implemented in GESTE, with a posterior probability of 0.29 (Table 5). However, the moderate σ^2 value representing an important deviation from the regression associated with the temperature model (0.26 ± 0.09) and the high posterior probability for the null model (0.52) might suggest only a weak effect of temperature on the genetic differentiation of populations, or perhaps no effect. Because of these results, we did not speculate further on the possible role of this environmental factor in shaping the pattern of genetic variation. Indeed, environmental characteristics such as turbidity, water masses and temperature are features that may be relatively labile, even over short to moderate time periods (1–50 years) in comparison to physical barriers. As such, it is plausible that clear genetic discontinuities were not associated with these variables because the locations of putative barriers associated with them have been fluctuating too much over time relative to time needed for genetic differences to accumulate. Also, it is obvious that such characteristics would be less efficient than physical barriers in restricting fish movements and gene flow.

In addition to physical barriers, the genetic discontinuity identified between the north and the south areas of Lake Saint-Louis was clearly associated with the environmental discontinuity caused by the junction of the two main physico-chemical distinct water masses found in Lake Saint-Louis: the brown waters deriving from the Lake des Deux Montagnes and the green waters coming from the

upper Saint Lawrence River. We hypothesize that the extent of gene flow between the two sides of Lake Saint-Louis and observed genetic differentiation may be influenced by the presence of important physico-chemical differences, which may lead to partial reproductive isolation between these two populations, perhaps caused by differential selective pressures associated to contrasting environments. Differences in metal and organic contamination between south and north sector of the lake could also foster the extent of environmental differences. Namely, Dumont (1996) showed that yellow perch occupying the more contaminated south shore were characterized by lower density, poorer body condition and a later age at sexual maturity.

Discontinuity between spawning habitats also accounted for the extent of genetic divergence observed in the sector spanning from Boucherville downstream to Gentilly, the area for which a map representing the estimated surface of 'good spawning habitats' for yellow perch was available. The longest distance without good spawning habitat was found between Contrecoeur and Île du Moine (spawning habitat fragmentation of 12.6 km). A genetic discontinuity depicted by BARRIER was associated to this region precisely, thus separating the Lake Saint-Pierre population from other upstream populations. This suggests that discontinuity in available spawning habitat for yellow perch may restrict gene flow by limiting dispersal of adult fish. However, as the spawning habitat ebbs and flows, and depends of variables that would change annually at least on the margins (including the three factors defining good spawning habitat: depth, current velocity, and vegetation surface), it is possible that the firmness of such a barrier could also change over time.

In contrast with features potentially restricting gene flow, other landscape characteristics of the Saint Lawrence River may potentially promote genetic connectivity between populations by enhancing dispersal, which could explain the relatively modest overall level of genetic differentiation observed in this study. Namely, the fluvial lakes found in the Saint Lawrence River are interconnected by zones of highly dynamic flow regimes, where the water masses flow in downstream direction until the end of Lake Saint-Pierre (CSL 1996). Unidirectional currents found in this nontidal fluvial section may promote dispersal of larval yellow perch (Laviolette 2004). The movement of pelagic larvae caused by currents or wind-driven transport of surface waters may enhance offspring mixing among spawning sites (Gerlach *et al*. 2001). Larval dispersal caused by gyral currents was also recently hypothesized by Miller (2003) to explain genetic differentiation of the yellow perch population of Green Bay from other areas of Lake Michigan. The fluvial estuary of the Saint Lawrence is characterized by pronounced semidiurnal tidal amplitudes, which is exploited for selective tidal stream transport by larval fish (Dodson *et al*. 1989; Laprise & Dodson 1989; Leclerc & Desgranges 2005), as well as by a maximum turbidity zone providing a rich planktonic and larval fish communities (Dodson *et al*. 1989; Laprise & Dodson 1989). These characteristics may also favour the dispersal of adult yellow perch and abundant food resources after the spawning season. This could explain why yellow perch migrate downstream in spring after reproduction before migrating upstream in September and October for over wintering and spawning the following spring (de Lafontaine *et al*. 2002). Interestingly, Böhling & Lehtonen (1984) documented similar feeding migrations for Eurasian perch that were associated with the migration of their prey (e.g. Baltic herring and smelt) in coastal waters of Finland. These authors also described differential homing behaviour in Eurasian perch to the spawning sites after winter, depending of the abundance of favourable shallow spawning areas in the surrounding. When perch were in locations with important spawning habitat area, homing to specific areas was observed less often and fish dispersed nearby only (Böhling & Lehtonen 1984). The same situation was observed in the Saint Lawrence River for yellow perch, which may explain genetic homogeneity observed in some areas, such as in the Lake Saint-Pierre, which offers large suitable areas for spawning (Morin & Côté 2003; Mingelbier *et al*. 2004). Here, dispersers from the Lake Saint-Pierre population could return from downstream feeding migration to the lake after winter, but not specifically to the same shore or the same location of the lake where they were found previously for spawning.

Relevance for conservation and management of yellow perch

Our conclusions about the existence of four genetically distinct populations of yellow perch in the Saint Lawrence River, also supported by previous studies of mark–recapture and population dynamics studies, have implications for the conservation and management of the species. First, our results support the consideration of these four populations as distinct biological units in subsequent conservation plans. Indeed, while the division of current management units based on six lake and fluvial sectors explained a significant proportion of genetic variance, the four groupings defined in this study increased the proportion of explained genetic variance. This analysis also allow to identify population boundaries that could not be defined intuitively, such as the genetic discontinuity between south and north shore of Lake Saint-Louis coupled with genetic homogeneity between north Lake Saint-Louis and Lake des Deux-Montagnes, or the genetic homogeneity observed from Lake Saint-Pierre downstream to Quebec City. Although this remains to be fully investigated, these four populations most likely differ in terms of life-history traits (Dumont 1996), dispersal behaviour (Dumont 1996; de Lafontaine

et al. 2002), and perhaps physiological adaptations to cope with different habitats, all of which could be important for the species persistence in particular environments, and particularly so in response to exploitation (Taylor *et al*. 2003). This study also provided evidence for the role of various landscape features (e.g. dams, habitat fragmentation, changes in hydrodynamic features) in influencing fish movements and patterns of genetic diversity alike. This emphasizes the importance of mitigating human impacts resulting in loss of spawning habitats for yellow perch (e.g. Mingelbier *et al*. 2004). Naturally fragmented habitats can have some positive effects, for instance by reducing impacts of regional stochasticity or exploitation over the whole distribution range of the species. On the other hand, the distance between patches could hamper the recolonization process (Hanski 1998). Future attention should be given to spatio–temporal variation in habitat use and migration of yellow perch, and test whether this varies between sexes and life-history stages.

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This research is part of Émilie Leclerc's M.Sc. thesis, which concerns the landscape genetics of yellow perch (*Perca flavescens*) in the St. Lawrence River. This work is also part of a collective effort towards improving conservation scenarios for this species. Yves Mailhot and Marc Mingelbier are, respectively, senior fisheries biologist at Trois-Rivières and research director in Québec city for the Ministère des ressources naturelles et de la faune du Québec (MRNF), Canada. Louis Bernatchez supervised ÉL's M.Sc. thesis. LB's research interests focus on the understanding of patterns and processes of molecular and organismal evolution, and their relevance to conservation.

Supplementary material

The following supplementary material is available for this article:

Table S1 Genetic diversity observed at eight microsatellite loci for all 25 samples of yellow perch spawning groups analysed in the study. Allelic richness ($\bar{A}$), expected and observed heterozygosities (H_E and H_O) and correlation values of heterozygote deficit (F_{IS}) values are indicated. Asterisks indicate significant departures from Hardy–Weinberg equilibrium using the test procedure of Guo & Thompson (1992) after Bonferroni correction to maintain type I probability error at $\alpha = 0.05$ ($k = 25$; Rice 1989). Allelic richness ($\hat{A}$) was calculated for the smaller sample size ($n = 40$) using the fstat 2.9.3 software (Goudet 2001). Code locations are explained in Table 1.

Table S2 Multilocus pairwise θ values (Weir & Cockerham 1984) calculated using genetix (Belkhir *et al*. 2001) above diagonal and probabilities below diagonal (NS, not significant; *0.05; **0.01; ***0.001).

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