

Effects of dynamic landscape elements on fish dispersal: the example of creek chub (*Semotilus atromaculatus*)

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Abstract

Barriers along a watercourse and interconnections between drainage systems are dynamic landscape elements that are expected to play major roles in the dispersal and genetic structure of fish species. The objective of this study was to assess the role of these elements using creek chub (*Semotilus atromaculatus*) in the Mastigouche Wildlife Reserve (Québec, Canada) as model. Numerous impassable waterfalls and interconnections among drainage systems were inferred with geographic information systems and confirmed *de visu*. The analysis of 32 populations using seven nuclear microsatellites revealed the presence of three genetically distinct groups. Some groups were found upstream of impassable barriers and in adjacent portions of distinct drainage systems. Admixture among groups was also detected in some populations. Constraining phylogenetic procedures as well as Mantel correlation tests confirmed that the genetic structure is more likely to result from interconnections between the drainage systems than from the permanent network. This study indicates that landscape elements such as interconnections are of major importance for circumventing impassable barriers and colonizing lakes that are otherwise inaccessible. Such an approach could be relevant for determining the origins of fish species (i.e. native vs. introduced) in the context of conservation.

Keywords: dispersal barriers, fish dispersal, genetic structure, interconnections, landscape genetics

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Introduction

Biogeographic and phylogeographic studies performed on freshwater organisms inhabiting formerly glaciated regions have revealed that numerous processes act together to influence their dispersal (Legendre & Legendre 1984; Wilson & Hebert 1996; Angers & Bernatchez 1998; Bernatchez & Wilson 1998; Rempel & Smith 1998; Castric *et al.* 2001; Triantafyllidis *et al.* 2002; Fraser & Bernatchez 2005; Poissant *et al.* 2005; Bertolo & Magnan 2006; Gagnon & Angers 2006; Girard & Angers 2006b). Because fish species dispersal is generally constrained to aquatic habitats, a correlation is usually observed between their distribution or genetic diversity and drainage systems (Angers *et al.* 1999; Castric *et al.* 2001; Costello *et al.* 2003; Stepiens *et al.* 2007). However, numerous processes may influence this

correlation, like the effects of glaciation, the presence of barriers and human-mediated translocations (Rempel & Smith 1998; Adams *et al.* 2001; Spens *et al.* 2007).

The presence of barriers along the watercourse acts as determinant factors on community structure (Snodgrass *et al.* 1996; Matthews & Robison 1998; Olden *et al.* 2001; Leibowitz & Vining 2003; Franssen *et al.* 2006; Lasne *et al.* 2007; Spens *et al.* 2007) as well as on genetic diversity (Angers *et al.* 1999; Reusch *et al.* 2001; Cook *et al.* 2002; Taylor *et al.* 2003; Knaepkens *et al.* 2004; Crispo *et al.* 2006). However, drainage systems are dynamic; they changed over time with spatial and temporal processes, so that the present-day networks are not always the best predictors of long-term lake interconnections. For instance, changes in drainage direction caused by isostatic rebounds have allowed colonization by founder groups from different origins at different periods of glacier retreat (Fraser & Bernatchez 2005). Similarly, intermittent waterways between drainage systems may also provide opportunities for species

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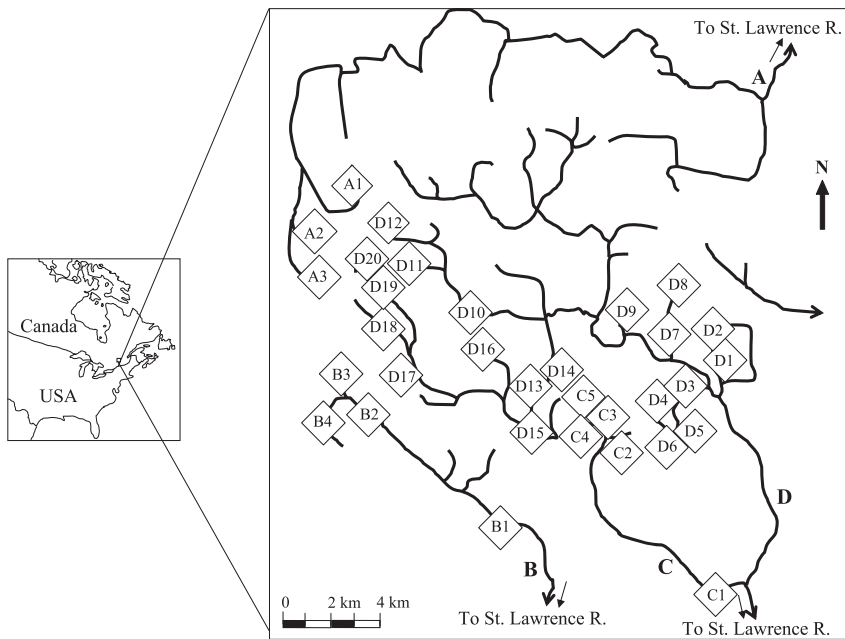


Fig. 1 Location of the study site and lakes. Drainage systems are identified by capital letters. Arrows indicate flow direction.

to disperse beyond the limit of a given system. The presence of such interconnections was invoked to explain dispersal throughout different drainage basins following the last glacier retreat (Legendre & Legendre 1984). On a small geographic scale, interconnections are expected to allow the dispersal of a given founder group into numerous drainage systems (Angers & Bernatchez 1998).

The objective of this study was to assess the role of barriers and interconnections on the dispersal of a fish species, the creek chub (*Semotilus atromaculatus*), within and among drainage systems. This objective was achieved in three steps: (i) barriers within and interconnections among drainage systems were identified with a geographic information system (GIS); (ii) genetic diversity was used to infer the population structure and dispersal patterns; and (iii) analyses comparing genetic results to the geographic information were performed to assess the role of permanent networks and alternate dispersal routes.

Creek chub is a native species in many regions of the northeastern North America (Scott & Crossman 1973). However, introductions by fishermen using creek chub as live bait are thought to have largely increased its present distribution (Scott & Crossman 1973). For instance, the distribution of creek chub in the Mastigouche Wildlife Reserve (Québec, Canada) is surprising: this species is completely absent in the northern part of the wildlife reserve while it is observed in nearly all lakes of the southern part [Québec Natural Resources and Wildlife (MRNF), unpublished data]. Most of the wildlife reserve area is included within a single drainage system (du Loup River), and distribution routes to both the southern and northern parts are blocked by impassable falls. Consequently, it has been assumed that populations of creek chub upstream of

impassable falls originated from such human introductions (Magnan & Fitzgerald 1982, 1984; Magnan 1988). An understanding of the effect of the landscape elements on the dispersal of this fish may thus be relevant for inferring its dispersal history as well as for determining whether it is a native or an introduced species.

Materials and methods

Study site and biological model

The Mastigouche Wildlife Reserve (MWR) is located on a plateau on the southern margin of the Canadian Shield (46°40'N, 73°25'W) in Québec, Canada. Its hydrographic system is a typical radial organization. The main drainage systems of MWR are only connected at the level of the St Lawrence River (Fig. 1), which is approximately 50 km downstream (straight-line distance). These systems are divided into distinct sections by the presence of several barriers such as waterfalls that constitute impassable obstacles for several fish species. However, the topology and geographical proximity of the drainage systems make it likely that numerous interconnections can occur among these systems. Several inconsistencies among official maps were detected and can be interpreted, according to Legendre & Legendre (1984), as changing connections due to seasonal freshets or changing water levels.

Assessment of barriers and interconnections

To identify interconnections between drainage systems, the study area was modelled using a 1:50 000 scale map, region 31-I, projection Nad 83 zone 18 North from the

Table 1 Characteristics of the study lakes. The sample size (N), altitude in metres above sea level [Alt (m a.s.l.)], corrected allele richness per locus and for all loci (A_c), total number of alleles (A), number of polymorphic loci (P), observed heterozygosity (H_o), Nei's gene diversity (H_E) and Hardy-Weinberg probability (HWE) for each population are given

Drainage System	Lake ID	Lake name	N	Alt (m a.s.l.)	Corrected allele richness (A_c)								Total	A	P	H_o	H_E	HWE
					Seat 26	Seat 61	Seat 97	Seat 407	Seat 411	Rhca 15	Rhca 20							
Matawin	A1	Supérieur	20	441	2.9	6.6	1.9	10.2	7.1	3.0	3.5	35.2	41	7	0.671	0.644	0.603	
	A2	Tremblay	20	442	3.0	4.4	1.5	7.3	5.6	2.9	3.0	27.7	31	7	0.634	0.565	0.129	
	A3	Bouteille	12	412	3.0	3.0	1.0	3.8	4.0	2.0	4.0	20.8	21	6	0.500	0.559	0.173	
Mastigou	B1	Petit William	12	332	2.8	2.9	2.0	7.0	3.7	2.0	3.0	23.4	25	7	0.417	0.474	0.131	
	B2	Cigale	20	428	3.0	3.9	2.0	4.9	3.9	2.0	2.0	21.7	22	7	0.606	0.586	0.886	
	B3	Caribou	20	431	3.0	3.9	2.0	5.4	4.9	2.0	1.9	23.0	25	7	0.514	0.544	0.801	
	B4	Saint Pierre	12	455	3.0	4.0	2.0	6.8	3.8	2.0	1.8	23.4	24	7	0.512	0.510	0.231	
Écorces	C1	Lambert	9	200	2.0	3.0	1.0	9.0	4.0	1.0	2.0	22.0	22	6	0.349	0.346	0.994	
	C2	Petit St Bernard	20	339	1.0	1.0	2.0	6.9	1.9	1.0	1.0	14.8	17	3	0.186	0.189	0.997	
	C3	Sac	20	367	1.0	1.0	1.5	6.6	1.0	1.0	1.0	13.1	15	2	0.100	0.123	0.082	
	C4	Minette	20	407	1.0	1.0	1.0	7.4	1.0	1.0	1.0	13.4	16	1	0.114	0.112	0.528	
	C5	Noir	20	412	1.0	1.0	1.0	8.3	1.5	1.0	1.0	14.8	17	2	0.143	0.130	0.874	
du Loup	D1	unnamed	19	210	2.9	3.9	1.5	9.3	5.8	1.0	3.1	27.4	34	7	0.429	0.440	0.154	
	D2	Vase	20	211	2.4	3.0	1.5	8.6	5.8	1.0	2.5	24.8	30	6	0.436	0.437	0.420	
	D3	Vanneau	18	239	1.6	3.5	2.0	12.4	5.5	1.0	3.5	29.4	36	7	0.444	0.460	0.825	
	D4	Rose	18	282	1.6	1.6	2.0	8.9	3.6	1.0	2.0	20.5	24	6	0.375	0.328	0.858	
	D5	Petit Carufel	20	292	1.9	1.0	2.0	10.3	2.9	1.0	2.0	21.2	25	5	0.336	0.342	0.341	
	D6	Vertnez	20	342	1.5	1.0	2.0	11.2	4.4	1.0	1.0	22.1	27	4	0.307	0.297	0.838	
	D7	Vaseux	20	239	2.0	4.9	1.0	11.5	4.9	1.0	3.0	28.3	32	5	0.518	0.521	0.086	
	D8	Pimbina	12	319	2.0	4.0	1.0	10.1	6.6	1.0	3.0	27.7	29	5	0.500	0.501	0.575	
	D9	Jones	17	282	1.5	3.8	1.5	8.1	4.7	2.0	1.0	22.7	27	7	0.403	0.381	0.570	
	D10	Théodule	12	380	1.0	1.0	1.0	7.5	1.0	1.0	1.8	14.3	15	1	0.131	0.133	0.941	
	D11	Grillon	11	451	1.0	1.0	1.0	2.9	1.0	1.0	1.0	8.9	9	1	0.039	0.064	0.111	
	D12	Oudiette	12	392	1.0	1.0	1.0	4.8	1.0	1.0	1.0	10.8	11	1	0.131	0.105	0.661	
	D13	Maubèches	20	399	1.9	1.5	1.5	7.8	2.0	1.0	1.9	17.7	22	6	0.207	0.201	0.998	
	D14	French	20	408	1.0	2.3	1.5	5.9	2.6	1.0	2.5	16.8	21	5	0.207	0.209	0.938	
	D15	Sans Bout	20	401	2.0	2.5	1.9	9.4	2.5	1.5	1.9	21.8	27	7	0.300	0.280	0.389	
	D16	Portage	12	447	1.0	1.0	1.0	5.8	1.0	1.0	1.0	11.8	12	1	0.143	0.115	0.760	
D17	Houde	12	452	1.8	1.0	1.0	6.7	1.0	1.0	2.0	14.6	15	3	0.179	0.170	0.545		
D18	Brisé	20	482	2.0	3.5	1.9	7.4	5.3	2.9	2.3	25.2	30	7	0.400	0.414	0.747		
D19	Vénus	20	457	1.0	1.9	2.0	7.5	2.9	1.8	2.0	19.0	20	6	0.314	0.304	0.993		
D20	Grosse	10	461	2.0	3.0	1.0	5.0	3.0	1.0	3.0	18.0	18	5	0.243	0.266	0.748		

National Topographic Data Base (NTDB) of Canada. The GIS program SIGIS 2.53 (Daoust & Jean 2007) was used to collect altitudinal data and geographic coordinates of sampled lakes and to analyse the configuration of drainage systems as well as the numerical elevation model. The absence of creek chub, determined previously by extensive fishing efforts (MRNF, unpublished data), in the northern part of MWR was used to determine the slope gradient over which this species cannot disperse upstream: previous studies have found that a slope gradient over a given distance may constitute a barrier to dispersal (Kruse *et al.* 1997; Adams *et al.* 2001). Afterwards, this limit was determined for the whole MWR and was considered as an effective barrier to upstream dispersal within a watercourse (e.g. waterfalls). The absence of this limit between drainage systems indicates that the slope is not great enough to

prevent dispersal and was thus considered as a potential two-way connection (symmetric dispersal). The presence of a limit between drainage systems may be interpreted as a potential one-way connection when a barrier between drainage dispersal is only present for one of the drainage systems (asymmetric dispersal). Drainage systems are considered isolated when the limit is detected on all neighbouring networks. The presence of these interconnections was further investigated by aerial surveys during the freshet period, when the water level was at its maximum.

Sampling and DNA analyses

Creek chub was sampled in 32 lakes from the main MWR drainage systems (Table 1, Fig. 1). Populations were

selected to assess the effects of waterfalls (downstream vs. upstream) and interconnections among drainage systems inferred as described in the previous section. Nine to 20 individuals per population were sampled, for a total of 538 individuals. A distant population located in a distinct hydrographic system (Lake Croche, 45°59'24"N, 74°0'19"W), 85 km southwest of MWR, was sampled and used as an outgroup for phylogenetic analyses.

A piece of the caudal fin was removed and preserved in 95% ethanol for DNA extraction by proteinase K digestion followed by phenol-chloroform purification and ethanol precipitation (Sambrook *et al.* 1989). Seven nuclear microsatellites were used for genetic characterization. Of these, Rhca15 and Rhca20 were designed for *Rhinichthys cataractae* (Girard & Angers 2006a) while Seat 407 and Seat 411 were designed specifically for *Semotilus atromaculatus* (Skalski & Grose 2006). Other loci were specifically designed for this study; these are Seat 26 (primers forward 5'-TCGACTCT-GTYGCTGTAGC-3' and reverse 5'-ATGTGATGAACGAC-CTGG-3'; GenBank Accession no. FJ434233), Seat 61 (primers forward 5'-GGCTAATTAATAATCTTCTCC and reverse 5'-NNTCGACGTCCCAGCACC-3'; GenBank Accession no. FJ434234), and Seat 97 (Angers & Schlosser 2007). Polymerase chain reaction amplifications were carried out in a volume of 12.5 µL containing 1.5 mM/L of MgCl₂, 2.5 nM/L of each dNTP, 0.3 µM/L of each primer, 0.2 U of *Taq* polymerase, 1.25 µL of 10× *Taq* polymerase buffer (Invitrogen Corp.) and approximately 20 ng of DNA. Reaction conditions were as follows: an initial denaturation of 30 s at 92 °C followed by 45 cycles combining 15 s at 92 °C, 15 s at 48 °C and 30 s at 68 °C, and a final extension of 2 min at 68 °C. Amplification products were separated on a denaturing 6% polyacrylamide gel (19:1 acrylamide:bis-acrylamide) and revealed using silver nitrate staining.

Characterization of population diversity

Genetic diversity was assessed by total allele richness (A), corrected allele richness (A_c), gene diversity (H_E ; Nei 1987) and the number of polymorphic loci (P) using FSTAT (Goudet 2001). Observed heterozygosity (H_O) was calculated with Genetix version 4.05.2 (Belkhir *et al.* 1996–2004). Departures from Hardy-Weinberg and genotypic equilibria were tested using GenePop version 4 (Raymond & Rousset 1995).

The population structure was inferred using two different approaches. The first method, proposed by Pritchard *et al.* (2000), identifies different groups of genetically similar populations. A model with admixture and correlated allelic frequencies was assumed with a length of burn-in, and Markov chain Monte Carlo (MCMC) of 10 000 and 10 iterations for k -group, 2 to 10 groups, was performed using the program Structure 2.1 (Pritchard *et al.* 2000). After different simulations, Evanno *et al.* (2005) consider that a length of burn-in and MCMC of 10 000 is sufficient to get a

good estimation of number of k -group and the appurtenance of individuals to these groups. k was first selected according to the α_1 and $\ln P(D)$ values given in the summary of the simulation window. When the value of $\ln P(D)$ reaches a plateau, the lowest number of k -groups associated with it was selected as the group division. This number of k -group was confirmed using the method of Evanno *et al.* (2005). Groups used in further analyses were formed by averaging the results of 10 iterations. A rooted phylogenetic tree was constructed with the neighbour-joining algorithm (Saitou & Nei 1987) using genetic distances estimated by the chord distance (Cavalli-Sforza & Edwards 1967). The robustness of the tree was assessed using the bootstrapping procedure with 1000 permutations of the Populations 1.2.24 software (Langella 2001). Genetic diversity partitioning was estimated using the hierarchical F_{ST} with the Excoffier method in Arlequin version 2.0 (Schneider *et al.* 2000).

Effects of barriers and interconnections on fish dispersal

To quantify the effects of barriers and interconnections on genetic structure, two different methods were used to take into account the topology of the drainage system and the geographic distances among lakes.

Assuming that the colonization process occurred in a stepwise fashion along the networks, a strong similarity is expected between the topologies of both the drainage system and the genetic distance/neighbour-joining (NJ) tree. This was assessed using the following combined approach of Nei (1995) and Angers & Bernatchez (1998): for a given topology, the branch lengths were estimated from the genetic distance matrix using the least-squares method (Cavalli-Sforza & Edwards 1967) without allowing for negative distances (using the tree option available in the FITCH option of the PHYLIP package, version 3.67; Felsenstein 1993). The sum of squares (SS) was then calculated for each topology and compared to the one expected from the NJ tree to provide the lowest SS for this set of genetic distances (Rzhetsky & Nei 1992). The more the SS of a given topology is similar to that of the NJ tree, the more likely it is expected to reflect the dispersal process. In addition to the topology of the permanent drainage system, alternative topologies were constructed to consider interconnections inferred formerly using GIS and aerial surveys. In order to conserve a dichotomic topology, the addition of an interconnection was counterbalanced by the addition of a barrier in the permanent network.

The colonization process and the exchange of migrants among populations are expected to provide a typical genetic signature in that the genetic differentiation is expected to be positively related to geographic distance (isolation by distance; Wright 1951). A matrix of geographic distances was constructed for each of the permanent and alternative

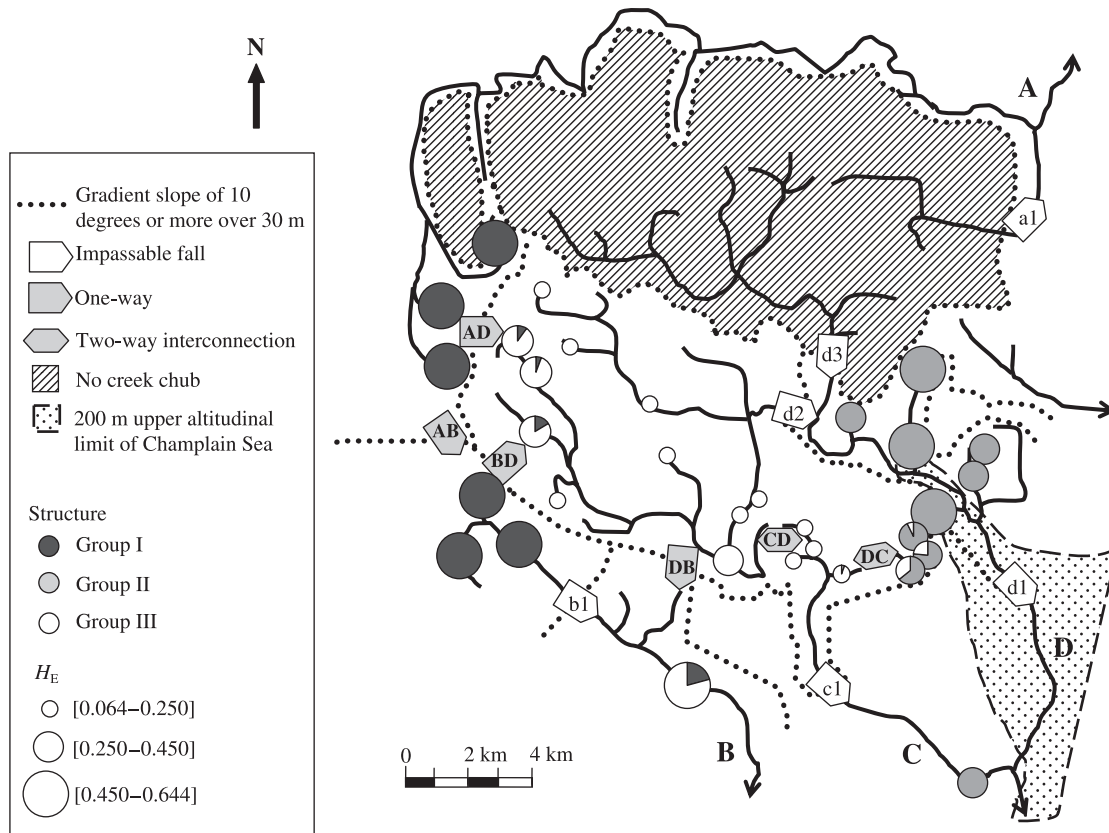


Fig. 2 Distribution limit, genetic diversity (gene diversity, H_E) and structure (level of population differentiation) of creek chub populations. Impassable waterfalls are identified by a small letter and a number while interconnections are identified by the two capital letters of the drainage systems they join. The gradient slope is defined as 10 degrees or more over a distance of 30 m. The dotted zone is the upper limit of extension of the Champlain Sea.

drainage systems. The correlation between genetic distances and geographic distances among populations calculated according to a given topology was tested using a Mantel (1967) test with 1000 permutations (available in the R program of the *vegan* package, based on Legendre & Legendre 1998). A similar Mantel test between genetic distance and topology was also performed to verify whether the results of the constrained tree are congruent with those resulting from the first Mantel test. Binary matrices were constructed from the topologies of each network using the segments method detailed in Legendre & Legendre (1998). The Jaccard distance index was used to calculate the distance matrices from binary topology matrices.

Results

Barriers and interconnections

Based on the drainage system characteristics expected to prevent dispersal of creek chub in the northern part of MWR, a slope gradient of 10 degrees or more over a distance of 30 m appears to represent an effective barrier to

dispersal (Fig. 2). This slope gradient was determined for all MWR drainage systems and allowed the detection of five barriers corresponding to waterfalls (Fig. 2). All creek chub populations, except A1, A2, A3, B1 and C1, are located upstream of these barriers. Six potential interconnections linking different drainage systems were also identified (Fig. 2). Based on the slope gradient, four of these are one-way and two are two-way interconnections. The occurrence of these interconnections was confirmed *de visu* by aerial surveys during the freshets.

Characterization of populations

The total corrected number of alleles per population is extremely variable, ranging from 8.9 (Population D11) to 35.2 (Population A1) (Table 1). Similarly, gene diversity over all loci varied by one order of magnitude, ranging from 0.064 (Population D11) to 0.644 (Population A1) (Table 1). None of the sampled populations showed a significant ($P > 0.05$) deviation from Hardy-Weinberg expectations, indicating that within a given lake, individuals were drawn from a single panmictic population.

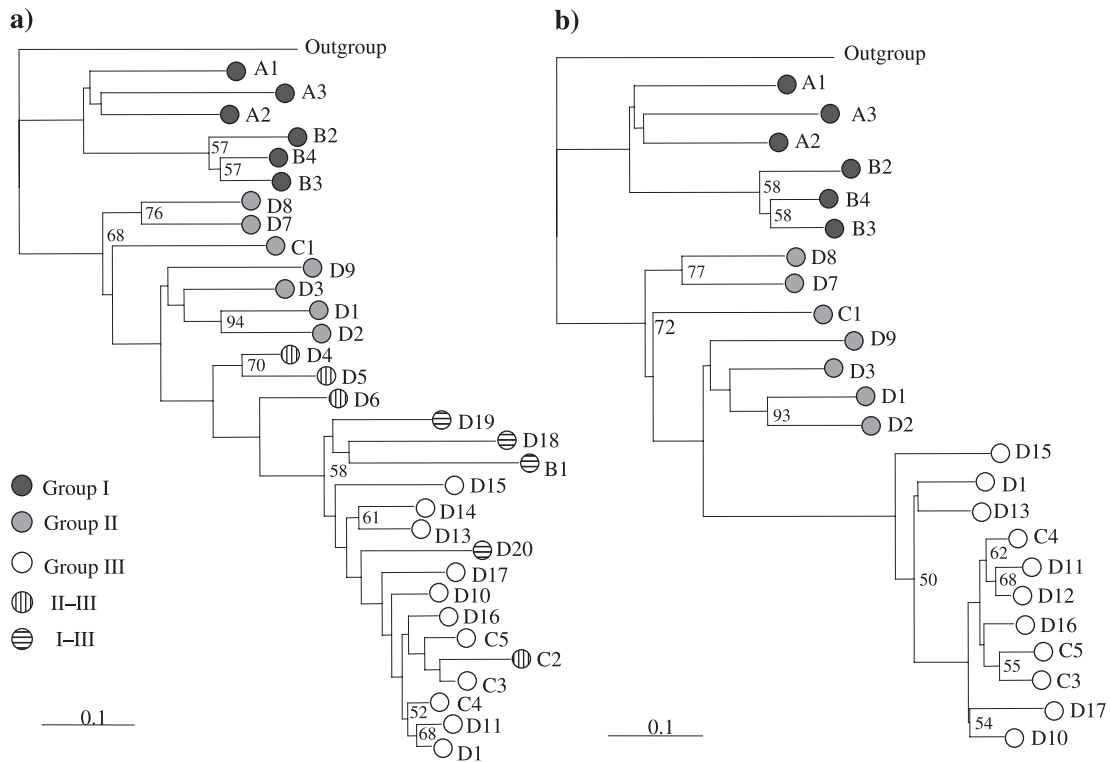


Fig. 3 Relationships among populations of the three groups as determined by rooted NJ trees: (a) with all populations; (b) without admixed populations. Only bootstrap values > 50% are indicated.

Table 2 AMOVA results for the three groups without admixed populations. d.f., degrees of freedom

Source of variation	d.f.	Sum of squares	Variance component	% of variation	Fixation index
Among groups	2	548.656	1.04665	44.01	0.44006
Among populations within groups	21	104.339	0.11410	4.80	0.08568
Within populations	772	940.042	1.21767	51.20	
Total	795	1593.036	2.37842		

As seen by the positions of populations along the watercourses (Fig. 2), the distributions are clearly not random. Populations downstream from barrier d2 exhibit a significantly higher diversity than those located upstream ($A_c = 24.9$, $H_E = 0.412$ vs. $A_c = 14.581$, $H_E = 0.160$; Wilcoxon Mann-Whitney test, $P > 0.001$), highlighting the importance of this barrier on dispersal. However, the presence of such a barrier does not necessarily result in low genetic diversity upstream. For example, populations upstream from barrier b1 (B2–B4) exhibit a level of diversity similar ($P = 0.7$ for A_c ; $P = 0.4$ for H_E) to those with no barrier in drainage system A. Surprisingly, an increase in diversity was observed in some populations upstream barrier d2. In these last two cases, interconnections near these populations may be responsible for gene flow between these systems.

Genetic structure

Three distinct genetic groups (hereafter referred to as I, II and III) were identified by the program Structure 2.1 as an optimal solution (Fig. 2). This population structure is supported by the NJ tree (Fig. 3): the low bootstrap values indicated that the MWR populations are not strongly differentiated. Most populations display a genetic contribution from a single group (Fig. 2). The hierarchical analysis of genetic variance (Table 2) revealed a high and significant F_{CT} estimate (0.44) but a low F_{SC} (0.09), indicating that most of the genetic variation occurs among groups.

Group II populations are restricted to the downstream part of du Loup River (systems C and D, Fig. 1). Interestingly, populations of the other groups are present in more than one drainage system (Table 1; Fig. 2). Group I populations

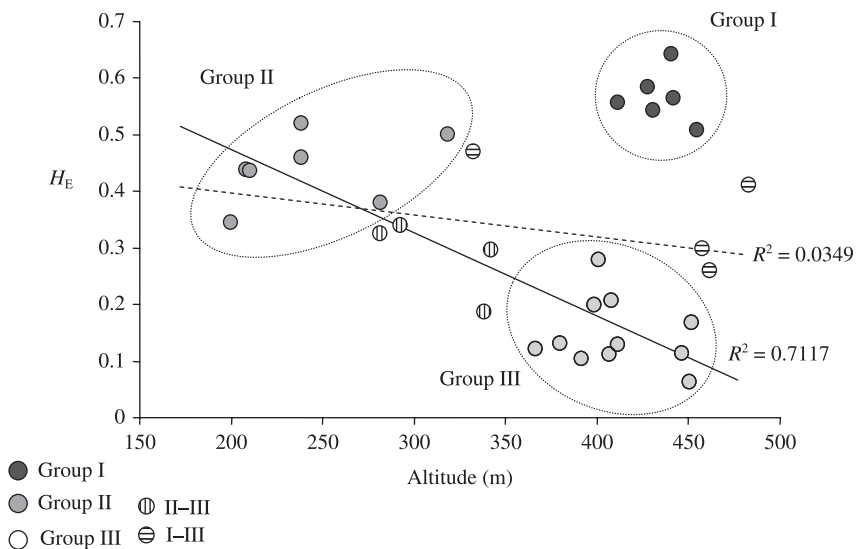


Fig. 4 Correlation between altitude and Nei's gene diversity (H_E). The dashed line represents the correlation when considering all populations while the solid line is the correlation for populations from groups II and III only.

Table 3 Genetic diversity of the three groups with admixed populations excluded. The number of alleles (A), corrected allele richness (A_c), number of private alleles, number of polymorphic loci (P) and Nei's gene diversity (H_E) are given for each group. The mean per population of each group was calculated for all estimators

Group	A	A_c	Private alleles	P	H_E
I	26.6	24.85	9	6.80	0.57
II	30.03	26.04	13	6.14	0.44
III	16.38	14.35	1	2.73	0.15

are detected on both sides of interconnection AB, in systems A and B. Similarly, group III populations are found on both sides of interconnection CD, in the upstream part of drainage systems C and D.

Some populations display a genetic contribution from more than a single group (Fig. 2). Admixtures between groups I and III were detected in populations D18, D19, D20 and B1 while the presence of both groups II and III were detected in C2, D4, D5 and D6. These results were confirmed by the reclassification of individuals (data not shown) using the GeneClass software (Piry *et al.* 2004). According to the distant positions of groups I and III in the phylogenetic tree (Fig. 3), the occurrence of both groups within a given population can only be the result of gene flow and hybridization. The contribution of group I to populations D18, D19 and D20 can be explained by migration via the interconnections AD and BD, while the contribution of group III to population B1 can be explained by migrations via interconnection DB.

The first NJ tree revealed that groups II and III are connected to each other by populations with contribution from both groups (Fig. 3a). Phylogenetic analyses performed

after removing populations with contributions of multiple groups showed a similar relationship (Fig. 3b), indicating that groups II and III were not brought together artificially due to the presence of these populations. In addition, genetic diversity is extremely low for group III when compared to group II (Table 3) and nearly all alleles detected in group III are present in group II. These two groups share 34 alleles while group II has 13 private alleles and group III has only one private allele. Taken together, these results indicate that group III was derived from group II, following a strong founder event (Fig. 4).

The origin of group III could be explained by three different scenarios. In the first scenario, the group C resulted of a drastic founder effect occurred with dispersal through waterfalls d2. The founders then colonize the upstream part of drainage system D. They use the interconnection CD to colonize system C and then DC to reach this part of system D and hybridize with group II in populations D3 to D6. The second scenario is similar except that the drastic founder effect occurred with dispersal through waterfall c1 to first colonize drainage system C and then system D by interconnection CD. The third scenario suggests a gradual reduction in the number of founders in populations D3 through D6. Interconnections DC and CD are then used respectively to colonize drainage system C then the upper part of system D. No hybridization between groups II and III occurs in the third scenario because group III is progressively formed by the successive founder effects that come from colonization of lakes D3 to D6.

None of these scenarios can be rejected definitively, but the third scenario appears to be the most parsimonious because no hybridizations are required to explain the composition of the D3 through D6 populations. The gradient from population D3 to D6 and from populations C2 to C5 in the corrected allelic richness decreased progressively

Table 4 Results of the constrained trees and correlation with or without interconnections. Sums of squares (SS) and correlations for genetic distances in relation to topology and waterway distances are given. AB, CD and DC refer to interconnections between drainage systems used for the alternate network

	SS	Topology		Waterway distance	
		Correlation	<i>P</i> value	Correlation	<i>P</i> value
Without hybrids I–III	3.68518	–	–	–	–
Permanent network	64.43465	0.5699	< 0.001	0.6551	< 0.001
AB	63.80959	0.5837	< 0.001	0.7287	< 0.001
DC and CD	10.12069	0.8319	< 0.001	0.6899	< 0.001
AB, DC and CD	9.56560	0.8506	< 0.001	0.781	< 0.001

from 29.4 to 13.1 and the number of polymorphic loci decreased from 7 to 1. A very strong and significant correlation between genetic diversity (A , A_c , H_E , P) and altitude was detected along the transition from group II to III but not over all populations (Fig. 4). While the admixture between groups III and II would be expected to provide the same results, the absence of a linkage disequilibrium supports the third scenario. It is noteworthy that whatever the origin of group III is, interconnections DC and CD are required to explain the observed genetic structure.

Network analyses

Because the phylogenetic procedure used is not designed to take hybridization into account, hybrid populations B1, D18, D19 and D20 were discarded from the analyses as were any interconnections potentially associated with these hybridization events. For the same reason, only the third scenario was tested because it considers populations D3 through D6 as transition populations while scenarios 1 and 2 consider these populations as admixtures between two groups. A third NJ tree was thus inferred without populations B1, D18, D19 and D20 and was used for the rest of the analyses. Removing the hybrid populations from the analyses does not affect the topology (data not shown). The SS for the NJ trees without these four hybrid lakes is 3.68. When this tree is constrained with the topology of the permanent network, the SS is nearly 20 times higher (64.43) than that of the NJ tree. The alternative hydrographic topologies obtained using all interconnections provided an SS value of 9.57, similar to that of the NJ tree (Table 4). This difference revealed an important incongruence between NJ tree and the permanent drainage topologies.

The correlation between NJ and the drainage topologies revealed a similar trend, with a higher correlation when all interconnections were taken into account ($r = 0.85$) than when using the permanent drainage topology ($r = 0.57$). Finally, Mantel tests performed between genetic and geographic distances show a better correlation when all interconnections are included ($r = 0.78$) than when they are

not ($r = 0.66$). Altogether, these results indicate that the drainage network constructed with interconnections fits better with the genetic data than with the permanent network.

Discussion

Role of the permanent network and interconnections

This study revealed that the pattern of the genetic diversity of creek chub in MWR is only partially consistent with the permanent drainage network. While populations of a given drainage system section are genetically similar, as expected for recent divergence and/or extensive gene flow, numerous inconsistencies were detected. High diversity upstream from some impassable waterfalls and in some lakes of the first-order sections (upper part of the system), as well as the presence of a given group in more than one drainage system, cannot be explained by migrations within the permanent network. Such inconsistencies appear to be a signature of postglacial colonization (Angers & Bernatchez 1998; Poissant *et al.* 2005) or introductions (Adams *et al.* 2001; Bryan *et al.* 2005; Kawamura *et al.* 2006; Kelly *et al.* 2006).

However, the few interconnections between drainage systems detected with geographic tools and verified *de visu* may provide an explanation for all these genetic inconsistencies. Correlations between genetics and geographic factors explained a larger part of the variation when interconnections were included in the network. For instance, interconnection AB decreases the waterway distance from 350 km in the permanent network to 12 km with the alternate route and provides a stronger correlation between genetic and geographic distances. It is unlikely that chance alone accounts for the presence of populations from this group in two distinct drainage systems upstream of an impassable waterfall (b1).

Three of the six interconnections identified (AB, DC and CD) appear to have played an important role in the genetic structure of creek chub in MWR by allowing colonization

upstream of impassable falls. The other interconnections (AD, BD and DB) appear to have allowed further dispersal to drainage systems already occupied by creek chub, leading to hybridizations. Altogether, these interconnections allowed the dispersal of groups I and II–III throughout two and four distinct drainage system sections respectively. The landscape elements such as waterfalls and interconnections are thus of major importance in the modelling of genetic organization, as expected from previous studies (Taylor *et al.* 2003; Habicht *et al.* 2004; Knaepkens *et al.* 2004; Poissant *et al.* 2005; Crispo *et al.* 2006).

Creek chub dispersal

Phylogenetic analyses suggest that only two founder groups have colonized MWR (groups I and II), with group III being derived from group II by founder events. The high diversity of populations downstream from waterfalls c1, d2 and d3 suggests that group II originated from the drainage system D. These waterfalls appeared to be efficient barriers to dispersal as this group has not been detected upstream. One scenario is that creek chub circumvented impassable waterfall d2 and progressed via lakes D3 through D6. Interconnection DC allowed individuals to invade system C upstream of waterfall c1, then return to drainage system D by interconnection CD upstream of waterfall d2. The loss of diversity resulting from founder events due to altitude led to the differentiation of the group III, which colonized the upstream section of system D. Other scenarios have similar processes but could have differed in the intensity of genetic drift (progressive or instantaneous). However, it is clear that dispersal from downstream to upstream occurred only once since independent founder events cannot provide similar results.

Within group I, populations from drainage systems A and B are closely related on the NJ tree, with nearly all alleles from the system B population being present in those of system A. Barrier b1 blocked movements from the downstream section of system B, as shown by the absence of group II–III upstream. All these evidences suggest that group I dispersed throughout drainage system A, then used the one-way interconnection AB to colonize system B.

The one-way connection DB explains the presence of group III in a lake downstream from waterfall b1. Similarly, some individuals from group I in drainage systems A and B took one-way interconnections AD and BD to disperse into first-order lakes, increasing the genetic diversity in these lakes.

This dispersal scenario proposes a way by which fish can circumvent impassable obstacles by using interconnections. However, although creek chub dispersal throughout MWR drainage systems is well explained by the presence of the interconnections, its presence upstream of barrier d1

likely involved a different process. Waterfall d1 is above 200 m (Fig. 2), an altitude that represents the upper limit of the Champlain Sea that covered St Lawrence valley approximately 10 000 years ago (McAllister *et al.* 1988; Rempel & Smith 1998; Ochietti *et al.* 2001). The Champlain Sea played the role of a barrier to fish dispersal and influenced the genetic structure of longnose dace (*Rhinichthys cataractae*) another cyprinid species (Girard & Angers 2006b). However, the Champlain Sea also provided dispersal opportunities. For instance, brook charr (*Salvelinus fontinalis*) is thought to represent the only native species in MWR, using the Champlain Sea to reach high altitude drainage systems (Magnan & Fitzgerald 1982, 1984; Lacasse & Magnan 1993). While creek chub is not known as a euryhaline species, it has been presumed that the large amount of glacier meltwater flowing into the sea created a freshwater layer in the littoral zone (Legendre & Legendre 1984). Some freshwater fish like creek chub may have used this littoral layer to colonize systems at altitudes higher than 200 m.

The opportunities offered by the Champlain Sea and interconnections suggest that no human intervention is required to explain the presence of creek chub upstream of impassable waterfalls in MWR. In this study, no sign of successful introduction that substantially altered the genetic composition of the populations studied was detected, indicating that if fish were recently introduced, they failed to reproduce. Nevertheless, it is not possible to definitively reject the scenario of translocation by humans. For instance, the translocation of fish upstream of impassable waterfalls may represent an alternate explanation for the origin of group III in scenario 1 or 2 (see Results).

If translocations rather than interconnections are responsible of the genetic structure observed in MWR, the dispersal of creek chub via human introductions must have followed a stepping-stone pattern, with the origin of creek chub being near the point of introduction. For instance, group III fish must have been captured in a lake of drainage systems C or D and transferred toward a different nearby section, and this had to happen numerous times. It is most improbable that multiple independent introductions from one diversified source, such as group II, would give rise to multiple populations with the same genetic composition (Kawamura *et al.* 2006). However, considering the practice of bait fishermen, who could have used one or several group II lakes to catch bait fish when going to fish in group III lakes, or those of fishing clubs, which were reported to systematically introduce cyprinids as forage fish in some lakes of this area, translocation could be an alternative hypothesis to explain the genetic structure of creek chub from group III lakes.

If one considers the very high genetic diversity of creek chub populations upstream from barrier d1, the scenario of human-driven dispersal requires that a large number of individuals must have been successfully introduced

(the same conclusion is applicable to populations B2 to B4). After a period of time required to reach a high density, a few individuals would then have been translocated to a lake upstream of barrier c1 or d2. Finally, once creek chub had again reached a high density, individuals would have again been translocated to the remaining drainage systems. In addition, these transfers had to have occurred a long time ago: creek chub had already been reported in lakes upstream from barrier c1 in 1929 (Prévost 1959). Finally, in spite of these hypothetical multiple introductions elsewhere, creek chub were never introduced upstream of the barrier d3. Such a series of events appear unlikely; thus, colonization of group III creek chub lakes via lake interconnections is the more parsimonious hypothesis.

Conservation perspectives

The current status of creek chub as an 'introduced species' in some regions promotes their eradication in order to restore the ecological integrity of lakes. A major motivation for such restoration is that creek chub competes with brook charr (*Salvelinus fontinalis*), a species of economic interest in northeastern North America. Creek chub is more efficient at feeding on benthic prey than brook charr (Magnan & Fitzgerald 1982, 1984), and when living in sympatry with charr, fishing yield and production of trout are lower by 30 to 50%, respectively, compared to when living in allopatry (Magnan 1988; Lacasse & Magnan 1992; Bourke *et al.* 1999).

The results of this study provide the first indication of mechanisms allowing a natural dispersal of this species upstream of impassable waterfalls. Further investigations of the genetic structure over a larger geographic scale are required to confirm the introduced or native status of the creek chub in MWR. For this, characteristics other than the presence of impassable upstream waterfalls must be determined prior to the assessment of species status in the absence of historical information.

The results of this study are also relevant in the context of lake restoration. While dams and other obstacles to dispersal built at lake discharges and in upstream drainage systems prevent recolonization of restored lakes from downstream sources, interconnections can be used as alternative routes for dispersal. Thus, interconnections between drainage systems must be considered when planning the prevention of recolonization of restored lakes by undesirable species.

In conclusion, this study highlights the role of interconnections in the dispersal of creek chub. Our analysis of the genetic structure indicates that creek chub use interconnections to circumvent some of the impassable waterfalls that block dispersal routes to the upstream part of many drainage systems in MWR. The results also suggest that the presence of creek chub in MWR may be natural, although further studies will be required to definitively assess this.

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This study is the main part of the M. Sc. thesis of J. Boizard. PM major research interests are in understanding patterns and processes of fish communities, as well as population ecology and evolution. BA is interested in the evolutionary biology of aquatic organisms. More specifically his research program focuses on the understanding of interactions between ecological and evolutionary processes with landscape elements in generating the biodiversity distribution.
