

The contribution of newly established populations to the dynamics of range expansion in a one-dimensional fluvial-estuarine system: rainbow trout (*Oncorhynchus mykiss*) in Eastern Quebec

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ABSTRACT

Aim Rainbow trout (*Oncorhynchus mykiss*, Walbaum 1792) is an exotic salmonid invading eastern Canada. First introduced for recreational fishing in Ontario, Quebec and the Maritime provinces, the species is now spreading in salmon rivers located in Eastern Quebec, where its stocking is strictly forbidden. Newly established populations have been found along the St Lawrence Estuary. To effectively mitigate the potential threat the invasion poses to native salmonids, we aimed to document the invasion's origin and progress in the St Lawrence River and estuary. We first determined genetic origins among several potential wild and cultured source populations, found at the upstream and downstream extremities of the St Lawrence system. Thereafter, we studied the range expansion, predicting that the invasion process conforms to a one-dimensional stepping-stone dispersion model.

Location Recently invaded salmon rivers that flow into the Estuary and Gulf of St Lawrence in Quebec, and watercourses supporting naturalized populations (Lake Ontario, Lake Memphremagog and Prince-Edward-Island rivers).

Methods Rainbow trout from 10 potential source populations (wild and domestic strains) and 243 specimens captured in salmon rivers were genotyped at 10 microsatellite loci. Genetic origins of specimens and relationship between colonies were assessed using assignment analyses based on individuals and clusters.

Results Invasion of rainbow trout in Eastern Quebec is directed downstream, driven by migrants from upstream naturalized populations, found in the Ganaraska River (Lake Ontario), and, to a lesser extent, in Lake Memphremagog. Populations from the Maritime provinces and domestic strains do not contribute to the colonisation process. A recently established population in Charlevoix (Eastern Quebec) supplies other downstream colonies.

Main conclusions Rainbow trout is spreading from Lake Ontario downstream to Eastern Quebec using the St Lawrence River system as an invasion corridor. Range expansion in a downstream direction is driven by a more complex stepping-stone dispersion model than predicted. Management options to protect native salmonids include reducing the effective size of the Charlevoix population, impeding reproduction in recently colonized rivers, halting the upstream migration of anadromous spawners, and curtailing stocking events inside the stocking area.

Keywords

Biological invasions, fluvial estuarine system, naturalized populations, population assignment, rainbow trout, stepping-stone dispersion model.

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INTRODUCTION

The dynamics of species' range expansions, particularly those of exotic species invading new habitats, is of considerable fundamental and applied importance in wildlife ecology. The study of invaders' range expansion is of particular interest as the invasion success and their impact on native fauna and flora relies in part on the rate and extent of spreading. Landscape spreading will depend on habitat connectivity, but also on the dispersion ability of the species which relies on many factors, including reproductive strategies and modes of dispersion. Good invaders are believed to be fast growing, to have high fecundity, to reproduce asexually and to have fast generation times and effective long and short distance dispersal (Laurenson & Hocutt, 1985; Kolar & Lodge, 2001; Colautti *et al.*, 2006; Richards *et al.*, 2006; Theoharides & Duker, 2007). Various efforts have been made to develop predictive numerical models of the invasion process. In the case of *continuum models*, space is represented by a continuous coordinate system and range expansion usually takes the form of reaction-diffusion equations (Kareiva, 1990). These equations constitute the Fisher-Skellam theory and describe the temporal changes in population density according to the local population growth (r) and the diffusion coefficient (D). This theory implies that the rate of spread is a linear function of time and can be predicted quantitatively as a function of measurable life history traits affecting population growth and dispersal abilities (Hastings *et al.*, 2005). Such models distinguish two kinds of diffusion: neighbouring and long-distance diffusion. Neighbouring diffusion results from individuals moving to adjacent areas over varying distances. Invasion dynamics are mainly driven by rare long-distance dispersers (Begon *et al.*, 1996), that lead to the creation of daughter-populations or invasion foci. When dispersion is proceeding from several locations and implies several diffusion modes, spread follows a stratified (or hierarchical) diffusion. Stratified diffusion, usually observed in invasions, can be much faster than linear or exponential spread (Hengeveld, 1989; Shigesada *et al.*, 1995; Shigesada & Kawasaki, 1997). Besides continuous systems, habitat can also be viewed as a series of patches or colonies. In *island models*, all patches are equally accessible as there is no specification about the distances between them (Kareiva, 1990). Alternatively, *stepping-stone models* assume patches with fixed spatial coordinates and the exchange of individuals is restricted to adjacent colonies or populations. Such models allow studying the consequences of long-range versus short-range dispersal in terms of genotypic and phenotypic diversity (Kimura & Weiss, 1964; Kareiva, 1990). In cases where the distance between patches approaches zero, stepping-stone models can be interpreted as continuum models (Kimura & Weiss, 1964).

Most studies of the spatial spread of invasions have used continuum models [see Kareiva (1990) and Hastings *et al.* (2005) for a review; Brown & Stepien (2009)], describing dispersal as waves of invasion involving simultaneous colonization on a large invasion front, with expansion being accelerated in good habitats, and slowed in poorer ones

(Shigesada & Kawasaki, 1997). However, when invasion involves freshwater fishes, stepping-stone or island models may be more appropriate as species are often habitat-specific (only found in lakes or rivers for example). Even if they are not completely isolated, watercourses can be geographically quite distant, supporting discrete colonies or populations. As an example, Boyer *et al.* (2008) demonstrated that populations of hybrids between native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*, Girard 1856) and introduced rainbow trout (*O. mykiss*, Walbaum 1792) dispersed in the Flathead rivers (USA and Canada) according to a stepping-stone model. The authors found a reduction of rainbow trout admixture with upstream distance from a site containing a hybrid swarm where rainbow trout accounted for 92% of the genetic diversity.

Rainbow trout is one of the most widely introduced fish species in the world and its impact on native fish communities is of increasing concern. In eastern Canada, repeated and massive stockings have occurred since the end of the 1890s in the Great Lakes, in the south-western part of Quebec province, and in the Maritime provinces, leading to the establishment of some naturalized populations. In Quebec, stocking and farming of rainbow trout were restricted to specific zones, located upstream in the St Lawrence River (Fig. 1). Early in the 20th century, the naturalized populations were only found inside this area (such as in Lake Memphremagog, Lake Champlain and the St Lawrence River near Montreal). However, since the 1970s, adult rainbow trout have frequently been captured by sport fishermen in the eastern part of Quebec in Atlantic salmon (*Salmo salar*, Linnaeus 1758) rivers that flow into the St Lawrence Estuary, up to the eastern-most end of the Gaspé peninsula (Whoriskey *et al.*, 1981; Dumont *et al.*, 1988).

Establishment of rainbow trout in salmon rivers might threaten native fishes, particularly other salmonid species, mainly by increasing competition and predation pressures. Conservation and management of the indigenous fish fauna thus requires better knowledge of the origin and spreading mode of the invader. The main objective of this study was to establish the dynamics of range expansion by rainbow trout in Eastern Quebec waters, characterized by a large fluvial-estuarine system. This one-dimensional system dictates that the species expansion is constrained to a downstream and/or an upstream direction. We first aimed to establish if rainbow trout captured outside the stocking area originated from sources located upstream in the St Lawrence system (up to Lake Ontario) and/or from sources located downstream, in the Maritime provinces. Secondly, we aimed to establish if annual stocking programmes in Quebec promote the invasion process by sustaining high propagule pressure. We thus determined if invading trout were derived from domesticated lineages currently used for stocking or from naturalized populations. Finally, we tested the hypothesis that the stepping-stone model best described the rainbow trout invasion process. To do so, we determined the relative importance of recently naturalized populations known to exist in Eastern Quebec waters relative

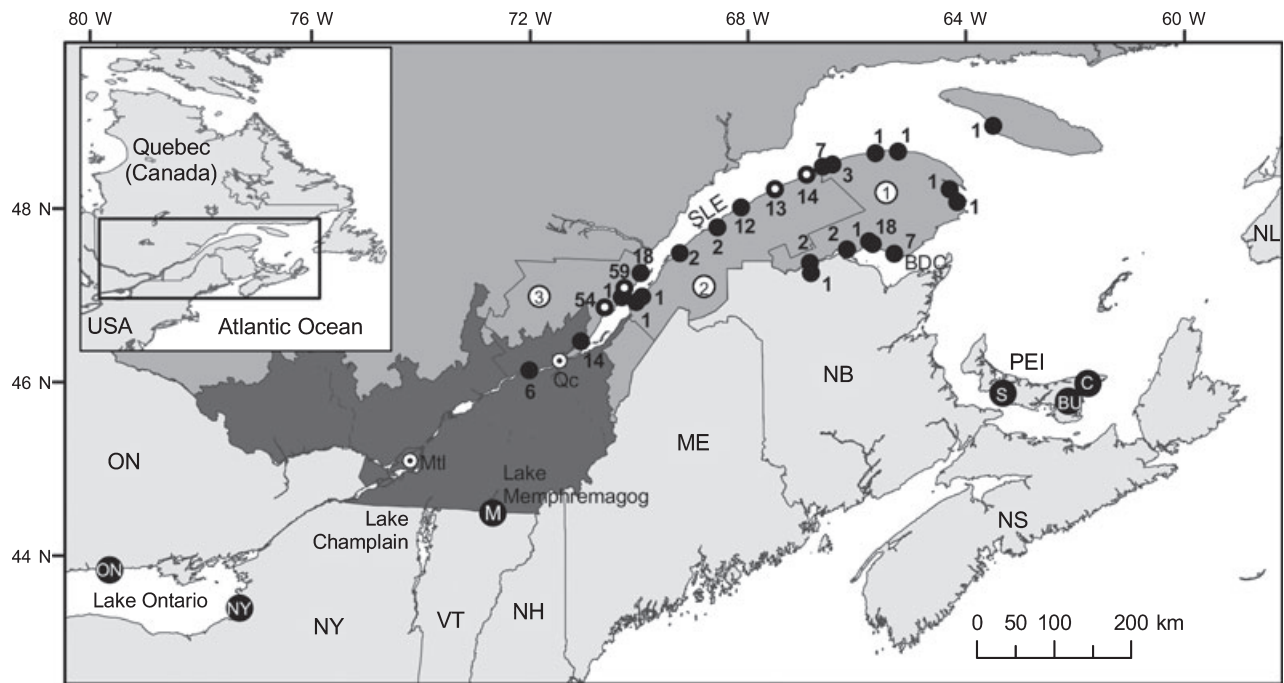


Figure 1 Map of the St Lawrence River system from Lake Ontario to Maritime provinces (Canada). Area where stocking of rainbow trout is allowed is shown in dark grey. Large black circles identify the location of wild source populations: Ganaraska R. (ON), Salmon R. (NY), Lake Memphremagog (M), Cardigan R. (C), Brudenell R. (BU) and Summerside Harbor (S). Sites where rainbow trout were sampled in Eastern Quebec between 2005 and 2007 are identified by small black circles. Associated numbers indicated the sample size. Rivers supporting self sustaining populations are marked by a white spot. Main regions bordering the St Lawrence Estuary (SLE): Gaspesia (1), Bas-St-Laurent (2), and Capitale-Nationale (including Charlevoix region; 3). Qc: Quebec City, Mtl: Montreal, BDC: Baie-des-Chaleurs. Other Canadian provinces: New Brunswick (NB), Prince Edward Island (PEI), Nova Scotia (NS), Newfoundland (NL) and Ontario (ON). USA states: New York (NY), Vermont (VT), New Hampshire (NH) and Maine (ME).

to those existing in previously stocked areas to the east and/or to the west of the target area.

METHODS

To achieve our objectives, we performed population assignment analyses based on DNA microsatellite polymorphisms using several potential source populations (wild and domestic) and rainbow trout captured in 2005–2007 in Eastern Quebec waters.

Sampling

Source populations

Ten source populations were selected for their potential contribution to the rainbow trout colonization in Eastern Quebec (Table 1). Two wild populations came from Lake Ontario, one reproducing in the Ganaraska River (ON, Canada), the other in the Salmon River (NY, United States). In Lake Ontario, rainbow trout has been stocked since 1878, both in Ontario (Canada) and New York (USA) (MacCrimmon, 1971), and the species is now listed as a native species (Kerr & Lasenby, 2000). Another wild population came from Lake Memphremagog, Vermont (USA). This lake was one of

the first watercourses, with Lake Champlain, to be stocked (in the late 1800s) by both Quebec and Vermont agencies (L. Gerardi & K. Kelsey, Vermont Fish and Wildlife Department, pers. comm.). Lake Champlain was another potential source population. However, as this lake is stocked with rainbow trout from either Salmon River or Lake Memphremagog populations, we did not include this site among the source populations. In Lakes Ontario and Memphremagog, stocked juveniles are derived not only from wild populations (with egg fertilization and incubation in a hatchery), but also from domestic strains from USA and Canadian hatcheries. Historically, both anadromous (steelhead) and resident forms were stocked. In Lake Ontario, wild populations are known to be 'anadromous', even though they never have access to salt water, as fish migrate to the lake for growth and return to the tributaries for spawning (Scott & Crossman, 1974).

In Quebec, rainbow trout is also periodically stocked in diverse watercourses by municipalities, fishing associations or private owners. Therefore, two cultured strains were sampled for their importance in annual local stockings: (1) a strain from *Pisciculture Lac-des-Écorces*, a governmental hatchery and (2) a strain from *Pisciculture Jacques-Cartier*, a private hatchery. The latter buys its eggs from *Troutlodge Inc.*, a commercial hatchery located in the United States that provides eggs and juveniles to many small hatcheries in the province.

Table 1 Origin and characteristics of 10 potential rainbow trout (*Oncorhynchus mykiss*, Walbaum 1792) source populations.

Province/State	ID	Fish farm/water-body	N	Form	Strain characteristics
Quebec	M	Lake Memphremagog	50	Steelhead	Wild population ¹
	LDE	Lac-des-Écorces hatchery	47	Resident	All-female
	JC	Jacques-Cartier hatchery	50	Resident	All-female
Ontario	ON	Ganaraska R., Lake Ontario	50	Steelhead	Wild population ¹
NewYork (USA)	NY	Salmon R., Lake Ontario	50	Steelhead	Wild population ¹
Prince Edward Island	PEI	Ocean Trout Farms	50	Steelhead	All-female
Island	PEI_C	Cardigan R.	27	Steelhead	Wild population
	PEI_BU	Brudenell R.	27	Steelhead	Wild population
	PEI_S	Dunk, Wilmot and Bradshaw rivers (Summerside Harbor)	50	Steelhead	Wild population
Nova Scotia	NS	Ocean Trout Farms	50	Steelhead	Both sexes

¹Supportive breeding with spawners from the same watercourse.

The Maritime provinces have also conducted rainbow trout stockings since 1887 (MacCrimmon, 1971), and some watersheds now support naturalized populations. Two cultured strains were obtained from the Atlantic provinces, one in Nova Scotia and one in Prince Edward Island. Wild populations were also sampled in five rivers in Prince Edward Island. No source population were obtained from Newfoundland as naturalized populations (mainly residents) are only found on the East Coast of the province (far from Quebec), and because rainbow trout cultured in marine cages (Bay d'Espoir) are all-female triploids (Chadwick & Bruce, 1981; Porter, 2000; Mullins, 2003). We attempted to obtain fish from New Brunswick, but legislation now restricts rainbow trout stocking and farming to the southwest part of the province, which is very far from Quebec, and the only wild population, found in the Shepody River, is now almost extinct (G. Cline, Area Chief Fisheries and Aquaculture Management in New Brunswick, pers. comm.).

Fish of unknown origin

In 2005, 2006 and 2007, sampling campaigns were organized with sport fishermen. They were invited to register their rainbow trout captures in one of 70 registration centers, almost all located in the offices of fishing associations and government establishments. Electrofishing surveys in target streams and collaborations with commercial fishermen and governmental employees also provided additional samples. A total of 25 fish were collected in 2005, 220 in 2006, and 164 in 2007. The 409 fish were mainly captured in Eastern Quebec, but some also came from more western regions where stocking is allowed. For the purpose of this study, only diploid rainbow trout captured in salmon rivers were kept for the analyses ($n = 243$, Fig. 1).

DNA extraction, amplification and sequencing

DNA was extracted using a modified salt-extraction protocol (Aljanabi & Martinez, 1997). Briefly, a small piece of muscle or

adipose fin tissue (conserved frozen or in 95% ethanol) was washed in distilled water and digested in 440 μL of salt homogenizing buffer [0.4 M NaCl; 10 mM Tris-HCl (pH 8.0); 2 mM ethylenediaminetetraacetic (EDTA, pH 8.0)] with 44 μL of 20% sodium dodecylsulphate (SDS) and 8 μL of 20 mg mL^{-1} proteinase K overnight at 37 °C with gentle rocking. The digestion was extracted with 300 μL of 6 M NaCl. The supernatant (600 μL) was transferred to fresh tubes and DNA was precipitated with an equal volume of cold isopropanol. After incubation at -20 °C for at least 1 h, the pellet was washed with 70% ethanol, dried and re-dissolved in 100 or 150 μL distilled water.

Variation at 10 microsatellite loci was assessed (Table 2). Seven multiplex systems were used for PCR, adapted from those developed by Chris C. Wilson and colleagues (Trent University, Ontario). PCR included 1.0 μL of extracted DNA, 10 μM of each primer, 1.1 μL of the 10 \times reaction buffer [100 mM Tris-HCl; 15 mM/L MgCl_2 ; 1% Triton X-100; 500 mM KCl], 0.22 μL dNTPs (10 mM each), 1.1 μL of the 10 \times BSA, 1.0 U *Taq* DNA polymerase and double-distilled H_2O to make up a total 11 μL reaction volume. The PCR conditions were a 11-min denature cycle (95 °C), followed by 35 cycles of a 1-min denature step (94 °C), a 1-min annealing step (59 °C) and a 1-min extension cycle (72 °C), followed by a final extension of 60 °C for 45 min to ensure that the amplified alleles have the '+A' extension added on. The forward primers were fluorescently labelled and the resulting dye-labelled amplified fragments were run on a genetic analyzer (Applied Biosystems Model 3100, Foster City, CA, USA) following manufacturer's protocols. Loci were combined in two groups of five microsatellites. Alleles were scored with GENESCAN 3.7.1 and GENOTYPER 3.7 softwares (Applied Biosystems).

Standard genetic analyses

Loci-specific and population-specific information, such as number of alleles, average number of alleles/locus, mean allelic richness, unbiased observed and expected heterozygosities (Nei, 1987) and inbreeding coefficient [F_{IS} , Weir & Cockerham

Locus	Multiplex	# alleles	A_R	H_E	Allelic range	Source
<i>Ots3</i>	A	15	14.897	0.645	121–153	Greig & Banks (1999)
<i>Ogo4</i>	A	12	11.995	0.777	115–147	Olsen <i>et al.</i> (1998)
<i>Omy1001</i>	C	24	23.902	0.920	169–235	Spies <i>et al.</i> (2005)
<i>Omy77</i>	B	21	20.945	0.869	79–139	Morris <i>et al.</i> (1996)
<i>One14</i>	C	10	10.000	0.782	148–166	Scribner <i>et al.</i> (1996)
<i>One8</i>	D	16	15.945	0.684	151–185	Scribner <i>et al.</i> (1996)
<i>Omy1011</i>	E	21	20.900	0.887	132–222	Spies <i>et al.</i> (2005)
<i>Omy27</i>	F	10	9.894	0.556	92–116	Heath <i>et al.</i> (2001)
<i>Ssa85</i>	F	33	32.897	0.874	92–180	O'Reilly <i>et al.</i> (1996)
<i>One2</i>	G	25	24.988	0.910	199–267	Scribner <i>et al.</i> (1996)
Overall	–	18.7	18.636	0.790	79–267	–

Table 2 Multiplex arrangement of 10 microsatellites and locus-specific information based on 694 specimens: number of alleles, allelic richness (A_R), unbiased expected heterozygosity (H_E) and allelic range.

(1984)] were determined with FSTAT 2.9.3 (Goudet, 1995) and EXCEL MICROSATELLITE TOOLKIT (Parks, 2001). The number of distinct source populations was confirmed by clustering analyses using STRUCTURE 2.2 (Pritchard *et al.*, 2000), based on maximum LLOD ($\ln P(D)$). Populations were tested individually and grouped (up to 10 simultaneously). According to the number of populations tested in a same analysis, K varied from 1 to 15 (always three replicates). Burn-in period length and MCMC were set to either 100,000, 200,000 or 500,000 repetitions, adjusted according to K (increased with K) to ensure likelihood stationarity (Pritchard *et al.*, 2000). All populations were considered as distinct, except for some Prince Edward Island wild populations. Results led us to pool all fish from the three rivers that flow into Summerside Harbor as only one source population (PEL_S). GENETIX 4.03 (Belkhir *et al.*, 2004) and SMOGD (Crawford, 2009) were used to determine the extent of genetic differentiation [0 estimate of F_{ST} , Weir & Cockerham (1984), and D_{est} , Jost (2008)] between source populations, based on 1000 permutations. Hardy–Weinberg equilibrium on a per-locus basis and linkage disequilibrium between pairs of loci were tested with GENEPOP 1.2 [web version, Raymond & Rousset (1995)] for each source population. Markov chain parameters for both tests were set at 10,000 dememorizations, 1000 batches and 10,000 iterations. Significance threshold (α) was fixed at 0.01.

Rainbow trout origins

The most probable genetic origin of individuals was determined using population assignment analyses performed in GENECLASS2 (Piry *et al.*, 2004). This software determines to which population, among a specified set of potential source populations, an individual of unknown origin is most likely to belong. Parameters were set to 10,000 simulated individuals, and used the simulation algorithm (Monte Carlo) of Paetkau *et al.* (2004), and the criteria of Rannala & Mountain (1997). An individual was excluded from the assignment test (and thereafter considered as an unassigned fish) when its probability of belonging to any of the potential source populations was lower than 0.05 (α). The level of resolution of the test was

determined with a re-assignment method (*leave-one-out*) based on individuals from source populations.

Rainbow trout dispersion mode

Common methods to document stepping-stone dispersal involve testing for isolation by distance, or by examining the correlation between geographical distance from *mother* populations and admixture found in *daughter* colonies (Boyer *et al.*, 2008). However, as the rainbow trout invasion in Eastern Quebec is recent and ongoing, these methods cannot be used as there are only a small number of established populations and fish captured in other rivers are few and mainly consist of adult vagrants of various origins (see Results). Therefore, two alternative approaches involving different spatial scales were used in parallel to test the stepping-stone hypothesis. The first method exploited individual-level assignment and involved the addition to the assignment analyses of four new source populations recently naturalized in Eastern Quebec (Malbaie, Du Gouffre, Les Mechins, Matane), located both on the north and south shores of the St Lawrence Estuary (Fig. 1), in order to test for the presence of secondary invaders that could have contributed to the invasion process. The second approach involved a population-level analysis. We considered rivers as colonies (even in the absence of evidence for reproduction). Analyses consisted in determining the genetic relationships among colonies using clustering techniques.

Individual-based analyses

It has been known since the 1980s that rainbow trout reproduces in Malbaie and Du Gouffre rivers, located in the Charlevoix region on the north shore of the St Lawrence estuary. Analyses performed on fish captured in those rivers ($n = 113$) with STRUCTURE 2.2 revealed that they could be pooled and considered as only one population. We thus created a new source population, Charlevoix (CX), and added it to the population assignment analysis (GENECLASS2). Reproduction in Matane and Les Mechins rivers, located in

the Matane region (Gaspé Peninsula), has also been reported since 2007. According to STRUCTURE 2.2, however, pooling these rivers was not justified. They were thus included in the analyses as two distinct populations, despite their small sample sizes ($n = 13$ and 14 respectively).

Population-based analyses

In order to find clusters among the 26 colonies (rivers) in Eastern Quebec, we executed the program FLOCK (Duchesne & Turgeon, 2009) with the number of requested partitions k varying from 2 to 9. For each k -value, k reference samples (*refs*) were built and all specimens within each sample were assigned to these reference samples. Samples comprising a majority of specimens assigned to a single *ref* were themselves assigned to that *ref* as samples. Thus the scale of the assignment operation was upgraded from specimen to sample. Samples assigned to the same *ref* within the same k run were grouped together within an *association list*. These association lists then served to calculate pairwise distances between samples based on the following rules. First, compute the co-occurrence index between A and B samples as follows: $CI_{AB} = 2 (CO_{A,B}) / (O_A + O_B)$, where $CO_{A,B}$ = number of times that A and B are found together within all association lists over all k values, and O_A or O_B = number of times that A or B is found within all association lists over all k values. The distance proper is: $D_{AB} = 1 - CI_{AB}$. The rationale for this distance statistic is simply that, given samples A and B, the more closely related they are, the more likely they will be found within the same association list.

Several distance matrices, based on a random selection of association lists, were built from all pairwise sample distances and subsequently processed by the programs NEIGHBOR and DRAWTREE in PHYLIP 3.68 (Felsenstein, 2004) to obtain sample clusters and their graphical representation (unrooted neighbour-joining tree). Eleven such graphs were built and only those clusters that consistently appeared in the various graphs were retained for further analysis. As a cross validation, another unrooted neighbour-joining tree was built in POPULATIONS 1.2.30 (Langella, 1999), with the Cavalli-Sforza and Edwards chord distance method (D_c , based on allelic frequencies), with 10,000 bootstraps on individuals. To be clustered, rivers had to be grouped together in at least 50% of all replicated trees. For both methods, the minimum number of fish in each river was set to five individuals. Since the D_c measure does not correct for sample size bias and the number of specimens per population varied from 5 to 59, we conducted the same analysis on a modified dataset where we adjusted sample sizes ($n = 5-7$) by randomly removing specimens in populations with large sample size. We also performed clustering analyses using Bayesian genetic tools such as BAPS 5.2 (Corander *et al.*, 2003) and STRUCTURE. As results were similar for all algorithms, we only present the clusters obtained with POPULATIONS and the complete dataset.

In order to investigate the relationship between clusters, specimens of each cluster were assigned to the set of samples

comprising all other clusters and the most contributive source populations (see Rainbow trout origins section). Assignments were done according to Paetkau *et al.* (1995) based on the lowest LLOD threshold ($LLOD = 0$), i.e. each specimen was assigned to the target sample for which it showed the highest likelihood.

RESULTS

Standard genetic analyses

The total number of alleles per locus varied between 10 and 33, with an overall mean allelic richness of 18.6 (Table 2). Among source populations, Hardy–Weinberg disequilibrium was observed at *One14* and *One2* loci (in 6 and 8 source populations respectively). These two loci were excluded from the population assignment analyses as HW equilibrium is required by algorithms used in GENECLASS2 (note that all loci were used with FLOCK which is less restrictive). Linkage disequilibrium ($P < 0.01$) was found in 29 pairs of loci out of 450 (0.06), as would be expected by chance alone. The source population PEI_S, which pools rainbow trout from three rivers, presented the highest rate with linkage disequilibrium observed at 11 pairs of loci (24%). When problematic loci were excluded, we observed heterozygosity values (range 0.528–0.833) similar to those expected under random mating (range 0.540–0.823) in almost all populations (Table 3). Significant F_{IS} positive values ($P < 0.05$) were observed for two cultured populations only (JC and PEI). Mean F_{ST} value was 0.14 and ranged from 0.04 to 0.25, whereas mean D_{est} value was 0.40 [0.16–0.58] (Table 4).

Origins of the invasion

The level of resolution obtained with the 10 source populations was high (Table 5-A). We obtained 82% of correct re-assignments, which reached 86% when α was set to 0.01 (data not shown). The majority of errors were found among

Table 3 Population-specific genetic information based on eight microsatellites: average number of alleles/locus (A), mean allelic richness (A_R), observed (H_O) and expected (H_E) heterozygosities and inbreeding coefficient (F_{IS} , $P < 0.05$ are indicated in bold).

Population	n	A	A_R	H_O	H_E	F_{IS}
ON	50	11.1	9.704	0.755	0.785	0.038
NY	50	10.4	9.097	0.747	0.772	0.033
M	50	11.9	10.743	0.833	0.823	-0.012
LDE	47	5.6	5.142	0.643	0.635	-0.013
JC	50	6.3	5.517	0.753	0.665	-0.133
PEI	50	6.9	6.190	0.723	0.622	-0.163
PEI_BU	27	6.0	6.000	0.644	0.637	-0.010
PEI_C	27	5.1	5.125	0.528	0.540	0.023
PEI_S	50	6.6	5.989	0.663	0.656	-0.011
NS	50	5.5	4.978	0.576	0.557	-0.034

Table 4 Pairwise estimates of F_{ST} (above diagonal) and D_{est} (under diagonal) between source populations of rainbow trout (1000 permutations), based on eight microsatellites. Lowest differentiation values ($F_{ST} < 0.10$ and $D_{est} < 0.30$) are in bold.

	ON	NY	M	LDE	JC	PEI	PEI_BU	PEI_C	PEI_S	NS
ON	–	0.05	0.04	0.12	0.12	0.13	0.09	0.13	0.08	0.15
NY	0.25	–	0.05	0.09	0.14	0.16	0.11	0.15	0.10	0.20
M	0.22	0.27	–	0.12	0.13	0.15	0.11	0.14	0.10	0.17
LDE	0.41	0.32	0.45	–	0.20	0.22	0.14	0.19	0.14	0.25
JC	0.43	0.49	0.50	0.55	–	0.22	0.15	0.19	0.12	0.23
PEI	0.38	0.49	0.50	0.54	0.50	–	0.18	0.20	0.16	0.09
PEI_BU	0.29	0.44	0.38	0.42	0.40	0.46	–	0.06	0.05	0.17
PEI_C	0.40	0.47	0.41	0.58	0.47	0.42	0.16	–	0.07	0.16
PEI_S	0.30	0.39	0.36	0.47	0.32	0.37	0.16	0.19	–	0.15
NS	0.39	0.53	0.51	0.56	0.50	0.17	0.38	0.31	0.32	–

locations from the Maritime provinces, and about half of them were re-assigned to another Maritime source population. Almost all the other errors involved re-assignment to the Ontario population (ON). The bias of incorrect re-assignments towards ON would be explained if that population were the principal founding population. No fish from a western source population was re-assigned to a Maritime source population.

Table 5 Level of resolution analysis for source populations, based on eight microsatellites, according to the *leave-one-out* method ($\alpha = 0.05$). (A) Ten source populations used to determine rainbow trout origins. (B) Eleven source populations, including Charlevoix, used to test the stepping-stone hypothesis. The proportions of correct assignments are in bold. Complete population names and characteristics are given in Table 1. '?' refers to un-assigned proportions.

	Origin	<i>n</i>	Re-assigned population											
			ON	NY	M	LDE	JC	PEI	PEI_BU	PEI_C	PEI_S	NS	CX	?
(A)	ON	50	0.82	–	0.10	–	–	–	–	–	–	–	–	0.08
	NY	50	0.02	0.86	–	–	–	–	–	–	–	–	–	0.12
	M	50	–	–	0.94	–	–	–	–	–	–	–	–	0.06
	LDE	47	–	0.04	0.02	0.92	–	–	–	–	–	–	–	0.02
	JC	50	–	0.02	–	–	0.96	–	–	–	–	–	–	0.02
	PEI	50	0.04	–	–	–	–	0.92	–	–	–	0.02	–	0.02
	PEI_BU	27	0.04	–	0.07	–	–	–	0.81	–	–	–	–	0.07
	PEI_C	27	0.04	–	–	–	–	–	0.15	0.59	0.19	–	–	0.04
	PEI_S	50	0.20	0.02	–	–	–	–	0.08	–	0.64	–	–	0.06
	NS	50	0.12	–	0.02	–	–	0.18	–	–	–	0.64	–	0.04
(B)	ON	50	0.78	–	0.08	–	–	–	–	–	–	–	0.08	0.06
	NY	50	0.02	0.86	–	–	–	–	–	–	–	–	–	0.12
	M	50	–	–	0.94	–	–	–	–	–	–	–	–	0.06
	LDE	47	–	0.04	0.02	0.91	–	–	–	–	–	–	–	0.02
	JC	50	–	0.02	–	–	0.94	–	–	–	–	–	0.02	0.02
	PEI	50	0.04	–	–	–	–	0.88	–	–	–	0.02	0.02	0.04
	PEI_BU	27	–	–	0.07	–	–	–	0.78	–	–	–	0.07	0.07
	PEI_C	27	–	–	–	–	–	–	0.11	0.56	0.19	–	0.11	0.04
	PEI_S	50	0.12	0.02	–	–	–	–	0.08	–	0.62	–	0.10	0.06
	NS	50	0.10	–	0.02	–	–	0.16	–	–	–	0.62	0.08	0.02
	CX	112	0.21	0.01	0.04	–	–	–	–	–	–	–	0.72	0.02

Five source populations were identified (GENECLASS2, 10 000 simulated individuals, $\alpha = 0.05$), as contributing to the rainbow trout captured in Eastern Quebec: Ganaraska River (ON), Lake Memphremagog (M), Salmon River (NY), Brudenell River (PEI_BU) and Summerside Harbor (PEI_S) populations (Fig. 2A). The great majority of the fish were assigned to either the Ganaraska River population (48%, thereafter referred to as the Lake Ontario population) or the Lake Memphremagog population (23%). Only 1% of fish were assigned to the Prince Edward Island populations. Sixty-four specimens (26%) could not be assigned to any of the source populations under the assignment criteria we applied. Interestingly, about half of these specimens were caught in one of the four rivers sustaining newly established populations, the Malbaie River.

Rainbow trout dispersion mode

Individual-based analyses (GENECLASS2)

The level of resolution of the test was determined when Charlevoix (CX) was added as a source population (Table 5-B). We obtained 79% of correct re-assignments, which reached 82% when α was set to 0.01 (data not shown). Twenty-one percent of Charlevoix individuals were re-assigned to the

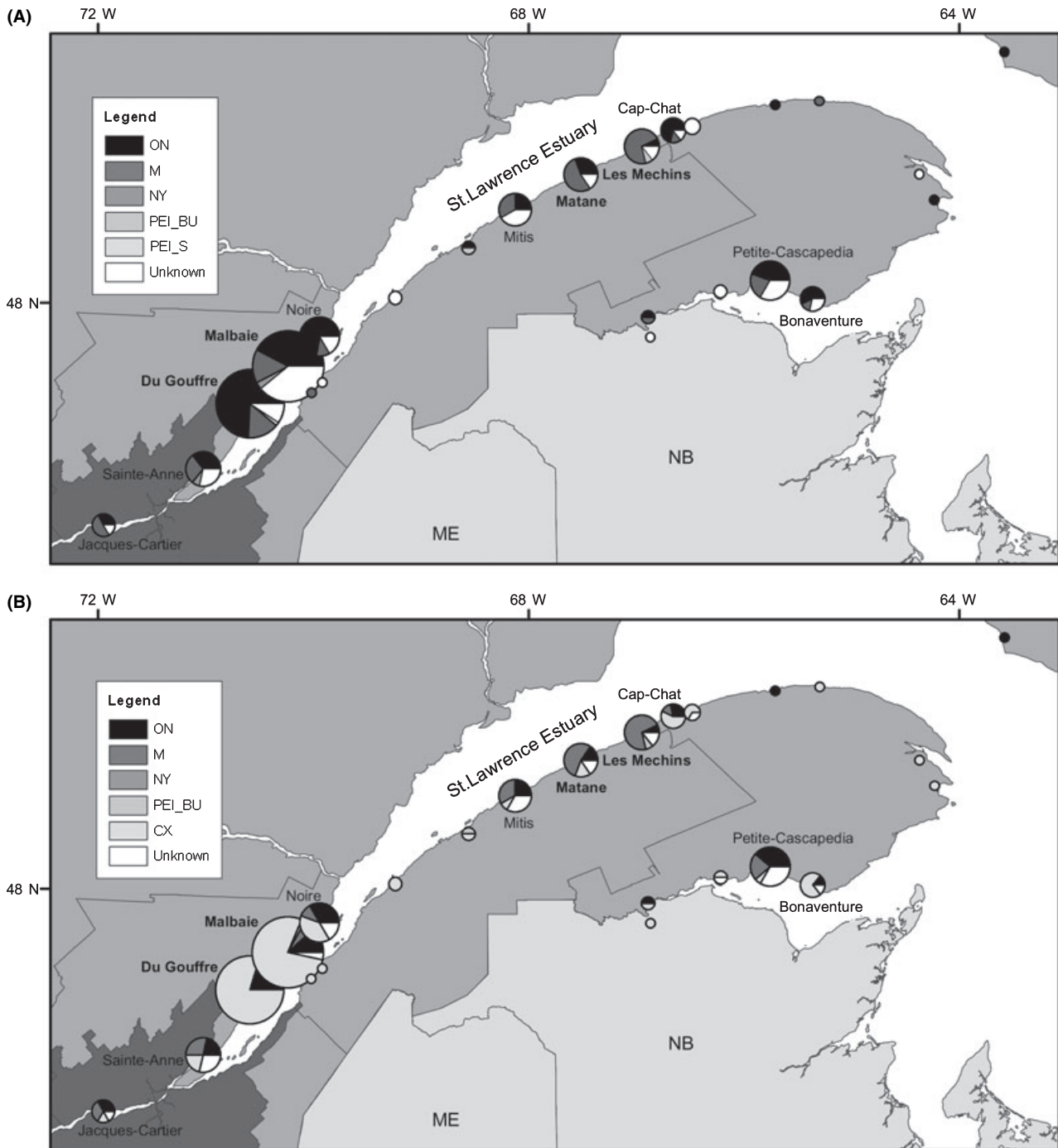


Figure 2 Genetic origin of 243 rainbow trout captured in salmon rivers located in Eastern Quebec between 2005 and 2007. Assignment analyses were performed with eight microsatellites and (A) 10 source populations, or (B) 11 source populations, including the newly established population of Charlevoix (Malbaie and Du Gouffre rivers). Stocking area is shown in dark grey. Rivers supporting self-sustaining populations are in bold. Circle size is proportional to sample size. Labelled rivers have more than five individuals. ON: Ganaraska River (Ontario), M: Lake Memphremagog, NY: Salmon River (New York), PEI_BU: Brudenell River (Prince Edward Island), PEI_S: Summerside Harbor (Prince Edward Island), CX: Charlevoix.

Ontario population, whereas 8% of Ontario fish were re-assigned to Charlevoix.

When Charlevoix was incorporated in the population assignment analysis as a new source population, 27 fish

captured outside Malbaie and Du Gouffre rivers, initially mainly assigned to Lake Ontario, were assigned to Charlevoix (Fig. 2B). Moreover, the number of fish previously un-assigned (excluding fish from Malbaie and Du Gouffre rivers) was

reduced by 30% as 11 of them were revealed to belong to this population. The results also showed that although trout captured in Malbaie and Du Gouffre rivers were mainly assigned to the Charlevoix population, some fish were still re-assigned to the Ontario ($n = 17$) and Memphremagog ($n = 4$) populations with higher likelihood. The addition of populations from Les Mechins and Matane rivers did not change the assignment results as no fish caught elsewhere was assigned to either of these populations.

Population-based analyses (FLOCK & Dc)

According to the population trees built with fish captured in Eastern Quebec, three clusters were identified (Fig. 3). A first group included Du Gouffre, Malbaie, Mare (large tributary of Malbaie River) and Noire rivers, all located in the Charlevoix region. Les Mechins and Matane rivers formed a second group. Finally, the last group comprised the Petite-Cascapedia and Bonaventure rivers, flowing into the Baie-des-Chaleurs. As there is no reproduction in that region, vagrants captured in both rivers presented a similar 'origin profile'. All three clusters were mainly assigned to Lake Ontario, followed by the Charlevoix population (Table 6). Percentage of assignment to any cluster other than Lake Ontario was always lower than 25%.

DISCUSSION

Despite huge introduction pressures around the world, the establishment of rainbow trout in new habitats appears difficult

(MacCrimmon, 1971; Fausch, 1988), being restricted by a series of physical and climatic factors including the number of secondary tributaries, the stream slope, the flooding period, and water temperatures (Fausch *et al.*, 2001; I. Thibault, R.D. Hedger, H. Crépeau, C. Audet & J.J. Dodson, unpublished data). This may explain why we find natural reproduction in only four rivers in Eastern Quebec. On the other hand, rainbow trout in Eastern Canada has been repeatedly and intensively stocked for many years in various watercourses. The spread of rainbow trout is facilitated by this variety of potential sources, as the number of foci is more important to invasion success than the size of individual foci (Hengeveld, 1989). Moreover, despite the species apparent difficulty in colonizing new habitats, it nevertheless possess several characteristic of good invaders (Moyle & Marchetti, 2006; Hänfling, 2007), such as tolerance to fluctuations in salinity and pH (Kerr & Lasenby, 2000) and excellent dispersal capacities, with an anadromous form (steelhead) that can migrate over many kilometers (Mongeau & Brisebois, 1982; Dumont, 1991).

Origins of rainbow trout in Eastern Quebec

The rainbow trout has been intensively stocked for many years in several streams and lakes in Southern Quebec, the Great Lakes and in the Maritime provinces. The origin of these fish has been very diverse, varying according to year and location. Therefore, it would not have been surprising to find that the invasion of rainbow trout in Eastern Quebec had many sources. Dumont *et al.* (1988) proposed that rainbow trout followed two routes to reach rivers in Eastern Quebec:

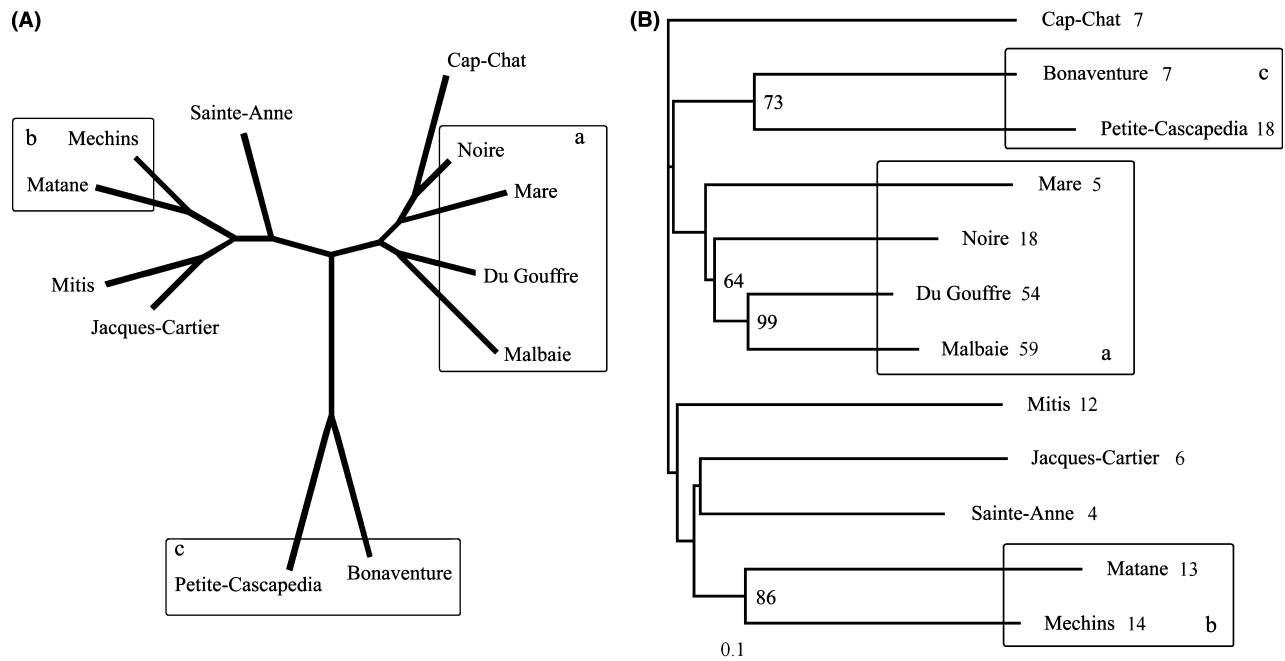


Figure 3 Unrooted neighbour-joining phylogenetic trees obtained with (A) FLOCK and (B) Cavalli-Sforza and Edwards distance methods. Rounded rectangles indicate clusters: (a) Charlevoix, (b) Matane-Mechins, (c) Baie-des-Chaleurs. Sample sizes are shown in graph B, and bootstrap values > 50% are presented at the nodes.

Table 6 Analysis of genetic similarity between clusters of rivers, based on re-assignment method: probability that each cluster belongs to one of the other clusters or source populations.

Origin	<i>n</i>	Re-assigned cluster				
		Charlevoix	Matane-Mechins	Baie-des-Chaleurs	Lake Memphremagog	Lake Ontario
Charlevoix	130	–	0.18	0.14	0.05	0.63
Matane-Mechins	27	0.11	–	0.07	0.07	0.74
Baie-des-Chaleurs	25	0.24	0.04	–	0.08	0.64

(i) from established populations in the upstream part of the St Lawrence River (such as Lakes Ontario, Memphremagog and Champlain) or (ii) from established populations and stocked fish from the Maritime provinces. To these possible colonization routes could be added the fish stocked yearly in Quebec province. Our population assignment analyses revealed that almost all rainbow trout captured in Quebec salmon rivers came from naturalized populations established in Lake Ontario (Ganaraska River population) and Lake Memphremagog. Only three fish appeared to belong to Maritime wild strains, Brudenell River (2) and Summerside Harbor (1), which represents only 1% of total captures. We are confident that they are not assignment errors as no fish from western source populations were re-assigned to Maritime populations in the analysis done to determine our level of resolution. Nevertheless, the quasi-absence of a Maritime signal clearly shows that the direction of the invasion process of rainbow trout is west-to-east, following the St Lawrence River.

The spread of rainbow trout in Eastern Quebec strongly relies on established (naturalized) populations. We demonstrated that all fish captured outside the stocking zones (excluding fish that we were unable to assign) originated from a wild population of steelhead trout. Therefore, even if local and private stockings occur yearly in many watersheds, it seems that the contribution of cultured strains to the invasion process is weak, as no 'hatchery signal' was found in Eastern Quebec. This may be explained by the use of sterile fish, that prevents reproduction and thereby establishment of domesticated rainbow trout in salmon rivers. In addition, even fertile hatchery females spawning in the wild tend to produce considerably fewer smolt and adult offspring *per capita* than wild females due to differences in egg production, timing of breeding and emergence, and genetic selection (McLean *et al.*, 2003, 2004). Also, most of the local stocking have a put-and-take purpose (release of catchable fish before a fishing event to increase immediate success), such that the majority of stocked fish are believed to be quickly recaptured and have little chance to migrate elsewhere and reproduce. Finally, stocked rainbows are often freshwater resident strains and present a lower potential to migrate outside their watershed to colonize eastern rivers, unlike individuals from wild populations, mainly composed of anadromous fish (L. Gerardi & K. Kelsey, Vermont Fish and Wildlife Department, pers. comm.; F. Whoriskey, Atlantic Salmon Federation, pers. comm.; I. Thibault, unpublished data).

Rainbow trout dispersion mode

Our results suggest that the invasion process of the rainbow trout in Eastern Quebec follows a complex stepping-stone dispersion mode along the St Lawrence River system, leading to the establishment of a few new self-sustaining populations in salmon rivers, which in turn produce vagrants that will eventually colonize other rivers. However, the process also involves invaders still dispersing from western source populations, although a recently naturalized population is a more important source of new colonizers to Eastern Quebec rivers. Thus, we demonstrated that rainbow trout first migrated downstream from established populations in Lake Ontario and, to a lesser extent, in Lake Memphremagog. Fish reached salmon rivers in Eastern Quebec and some established self-sustaining colonies in at least four rivers in the Charlevoix and Matane regions. According to individual-based analyses, the ultimate origin of these new populations is not the same, Les Mechins and Matane populations being more related to Lake Memphremagog fish, and Charlevoix rainbows being more similar to the Ontario strain. Furthermore, it appears that many rainbow trout originating from Charlevoix migrated to the East and are now found as far downstream as the Baie-des-Chaleurs region. For now, there is no evidence that Matane and Les Mechins populations contribute significantly to the continuing invasion by producing vagrants as no signal was observed when they were considered as source populations. Their establishment thus appears to be quite recent. However, we cannot discount the possibility that the small samples from these rivers may decrease population assignment success. Sample sizes were clearly too small to be representative of the genetic population diversity and in population assignment analyses, source populations should preferably include at least 30 individuals.

In a classical stepping-stone model, fish would have moved only between adjacent established populations (Kimura & Weiss, 1964). In the St Lawrence system, fish from at least three different populations (ON, M and Charlevoix) still continue to move far downstream and co-occur in many salmon rivers, thus forming multi-focal waves of invasion. This illustrates a complex dispersion process that is still in progress.

Consequence of the small temporal scale

The first observation of natural reproduction (captures of juveniles 0+) was in Du Gouffre River, in 1984 (Pelletier, 1985). Thus, the oldest self-sustaining population outside the

stocking area is *c.* 25 years old. Considering that rainbow trout first reproduces at *c.* 4 years of age (Scott & Crossman, 1974), < 10 generations have occurred since the founding of this population. Even if rapid genetic differentiation in salmonid populations is possible (Ayllon *et al.*, 2006), this population is still similar to its founding population ($F_{ST} < 0.04$ between Du Gouffre R. and Ganaraska R. populations). This small temporal scale implies that differentiation between *mother* and *daughter* populations is still low, possibly because of both the short time frame since the founding of Du Gouffre River as well as ongoing gene flow from Ganaraska River which may have introduced some bias in our analyses. This probably explains the 21 fish from Du Gouffre and Malbaie rivers that were assigned to either Ontario (15.0%) or Memphremagog (3.5%) populations, instead of to the Charlevoix population.

Fish of unknown origin

It was not possible to identify the genetic origin of some rainbow trout (11% when CX added) captured in 11 rivers. During the analysis performed to determine the level of resolution, we obtained a much lower rate of un-assigned fish (4%), indicating that the unidentified fish do not simply reflect the error margin of the test. We thus conclude that some source populations are probably missing from our analysis. It was not possible to sample all the potential source populations as some strains were unavailable and some populations are either extinct or unidentified. According to our results, it seems unlikely that the sources of these un-assigned fish are domestic strains. Rather, we suggest that these fish came from unknown wild population(s), established either upstream of Quebec City or recently established in the St Lawrence Estuary basin. The greatest number of un-assigned fish came from the Malbaie River. Genetic analysis revealed that Malbaie rainbows mainly originated from Lakes Ontario and Memphremagog. However, the high number of fish of unknown origin in that river also suggests that there might be an additional colonization source yet to be identified.

Concluding remarks

The introduction of rainbow trout in the western part of Quebec occurred many decades ago, but the species invasion in Eastern Quebec is a recent phenomenon, only observed in the last 35 years, and is still ongoing. We demonstrated that the invasion is driven by dispersal (most probably involving the anadromous steelhead ecotype) that originated from established populations in Lakes Ontario and Memphremagog. The invasion involves a complex stepping-stone dispersion mode along the St Lawrence River system, leading to the establishment of a few new self-sustaining populations in salmon rivers, which in turn produce vagrants that will eventually colonize other rivers. We also observed that invaders still continue to migrate from Lakes Ontario and Memphremagog, but the recently established population in Charlevoix is a more important source of new colonizers to Eastern Quebec rivers.

The protection of native salmonids in eastern Quebec requires some management initiatives aimed at reducing the eastward spread of rainbow trout. Such initiatives could include (1) reducing the effective size of the Charlevoix population through a targeted sport fishery, (2) impeding reproduction in the Matane and Mechins Rivers as the number of reproduction events are believed to be few and localized, (3) halting the upstream migration of anadromous spawners in the Matane River by better monitoring of the fish passage located near the river's mouth and (4) curtailing the establishment of new source populations by restricting repeated and massive stocking events inside the stocking area.

The algorithm FLOCK used in this study is now available at http://www.bio.ulaval.ca/no_cache/en/departement/professeurs/professeurs/professeur/11/13/ (last accessed 10 September 2009).

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BIOSKETCHES

Isabel Thibault's research interests are in understanding the displacements and interactions of fish species, and her current research involves the establishment of a monitoring network for freshwater fish populations in Quebec lakes.

Louis Bernatchez's interests relate to the understanding of patterns and processes of molecular and organismal evolution, and their relevance to conservation.

Julian J. Dodson's research interests focus on the ecology and evolution of life-history polymorphisms in fishes.

I.T. participated in the design of the study and carried out a part of the sampling, all laboratory analyses and drafted the manuscript. L.B. participated in conceiving the project and in the design of the study, and supervised all aspects of the molecular analyses. J.J.D. conceived and initiated the project, participated in the design of the study and drafted the manuscript. All authors contributed to the writing of the final version of the manuscript.

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