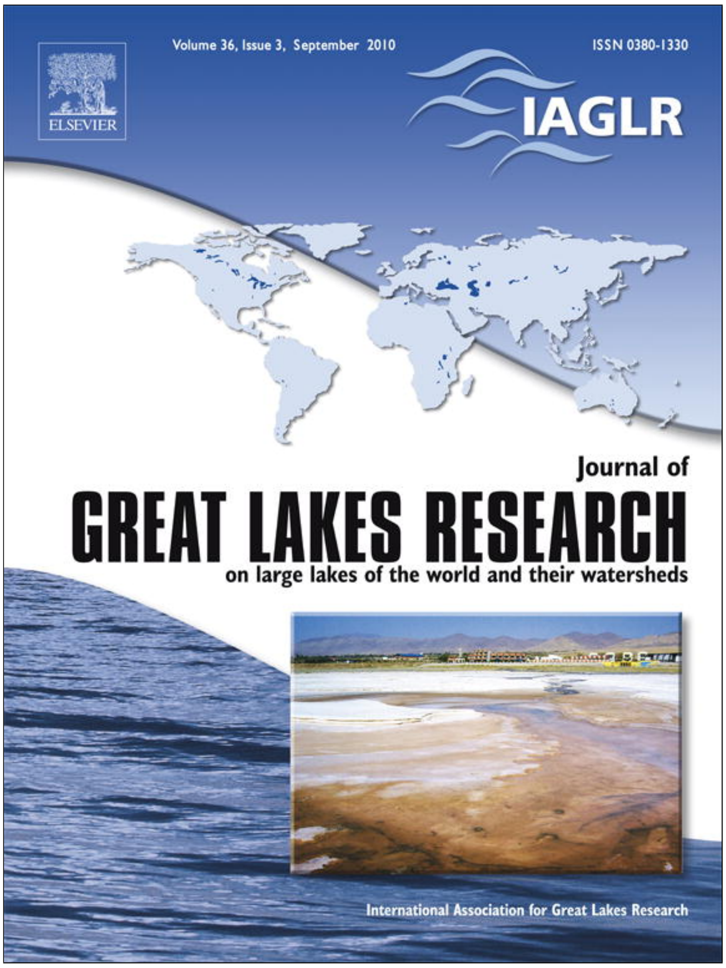
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The invasion of a large lake by the Eurasian genotype of common reed: The influence of roads and residential construction

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ABSTRACT

The Eurasian genotype of common reed (*Phragmites australis*) is one of the most aggressive plant invading North American wetlands. There is, however, little published evidence on establishment patterns of populations along lakes of the St. Lawrence River–Great Lakes watershed. We tested the hypothesis that the recent invasion of Great Lake Saint-François (Québec, Canada) by common reed was facilitated by a dense road system and by an intense residence construction activity along lakeshores. A total of 345 and 2914 reed stands were mapped along lakeshores, and along the road system of the study area, respectively. The probability of finding a reed stand on a lakeshore increases with the proximity of the lake's outlet, and of a paved road, but decreases with the proximity of a residence built since 1990. It is likely that common reed first spread along the road system, and that wind dispersal of seeds then favored the establishment of populations on lakeshores. Our model does not support the hypothesis that residential construction facilitated the establishment of reed stands, probably because the recent residential construction boom occurred essentially in the southern part of the lake, where the number of roadside reed populations is much lower than in the northern part (lower seed rain). The invasion of Great Lake Saint-François shows that the spread of the plant is not restricted to major river or road systems. Large or small lakes, if submitted to intense diaspore pressure, can also be at risk.

Introduction

Common reed (*Phragmites australis* (Cav.) Trin. ex Steud.; Poaceae) is one of the most aggressive aquatic plants invading eastern North American wetlands (excluding Florida). Large populations covering hundreds of hectares are abundant along the Atlantic coast of the United States (from Connecticut to Virginia) and in the Mississippi River delta (Rice et al., 2000; Warren et al., 2001; Lathrop et al., 2003; White et al., 2004; Philipp and Field, 2005; Chambers et al., 2008). The spread and expansion of common reed populations have been associated with the 19th century introduction of a Eurasian subspecies (*P. australis* subsp. *australis*), also known as 'haplotype M' (Saltonstall, 2002). This subspecies is particularly productive in wetlands that have been enriched with nitrogen from nearby agricultural sources (Bertness et al., 2002; League et al., 2006; Chambers et al., 2008). Haplotype M of common reed has serious negative impacts on the hydrology (Windham and Lathrop, 1999; Hanson et al., 2002; Osgood et al., 2003) and biodiversity (Benoit and Askins, 1999; Silliman and Bertness, 2004; Robertson and Weis, 2005; Hunter et al., 2006) of salt and brackish coastal marshes.

Common reed populations have recently expanded inland, and especially in freshwater marshes along the St. Lawrence River and on the shores of the Great Lakes (Wilcox et al., 2003; Hudon et al., 2005; Trebitz and Taylor, 2007; Tulbure et al., 2007; Whyte et al., 2008). Historical and genetic evidence suggests that haplotype M was introduced in the St. Lawrence River–Great Lakes watershed at the beginning of the 20th century (Lelong et al., 2007). Its spread along the St. Lawrence River was initiated in the 1960s (Lelong et al., 2007), but establishment of large populations only occurred in the 1990s and 2000s at Montréal (Grandes battures Tailhandier, Québec), Lake Erie (Long Point, Ontario; Old Woman Creek National Estuarine Research Reserve, Ohio) and Lake Michigan (Point au Sauble, Wisconsin). Common reed likely benefited from periods of low water level to locally expand populations (Wilcox et al., 2003; Hudon et al., 2005; Tulbure et al., 2007; Whyte et al., 2008). Studies on common reed have been mostly conducted in salt and brackish coastal marshes, and therefore causes of common reed expansion and its consequences on the hydrology and biodiversity of freshwater marshes are less well known. Common reed is likely to have a negative impact on the diversity of vascular plants (Farnsworth and Meyerson, 1999; Keller, 2000; Ailstock et al., 2001; Lavoie et al., 2003; Wilcox et al., 2003; Tulbure et al., 2007; Whyte et al., 2008), but there are almost no data on the impact of haplotype M on wildlife (fishes, amphibians, birds) diversity and reproduction. The only study (to our knowledge) that

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was conducted on the impact of the plant on animals of freshwater marshes (Long Point) has shown that common reed expansion may negatively affect some bird (rails, sparrows, waterfowl) and frog species, but may also benefit others, including voles and shrews (Meyer, 2003).

If the expansion of the haplotype M of common reed along shores of the St. Lawrence River and of Great Lakes has been documented, there is, on the other hand, very little published evidence on establishment patterns of large populations along other rivers and lakes that are present in the watershed. For instance, although common reed populations are scattered throughout the states of New York and Vermont, there are no data suggesting that stands of haplotype M are expanding along shores of Lake Champlain (the largest lake of these states). This is intriguing, since Lake Champlain functions as a conduit for exotic species exchanges between Hudson River, St. Lawrence River and Great Lakes (Marsden and Hauser, 2009). In Québec, where the northern tip of Lake Champlain is located, the dense highway system of the southern part of the province has strongly contributed to the spread of haplotype M, with roadsides acting as corridors and habitats (Lelong et al., 2007, 2009; Maheu-Giroux and de Blois, 2007; Jodoin et al., 2008). Lakes surrounded by roads should consequently be highly susceptible to invasion. To our knowledge, the only published evidence documenting such lake invasion comes from a study of Great Lake Saint-François in southern Québec, where 350 stands of haplotype M of common reed have recently (~10 years) established. Genetic data showed that seeds were primary diaspores responsible for establishment of common reed populations along shores (Belzile et al., 2010). In this paper, we examined probable causes and pathways of this invasion. Using a set of field and historical data, and a logistic regression model, we tested the hypothesis that the invasion of the shores of Great Lake Saint-François by the haplotype M of common reed was facilitated by the dense road system surrounding the lake (which provided corridors and habitats for the plant), and by the intense residence construction activity that occurred along lakeshores in the 1990s and 2000s (which provided suitable seedbeds for the invader).

Methods

Study area

Great Lake Saint-François is the third largest (51 km^2) lake in Québec south of the St. Lawrence River (Fig. 1). This lake must not be confused with Lake St. Francis (or Lake Saint-François), a widening of the St. Lawrence River near the Québec-Ontario border. Great Lake Saint-François drains a watershed of 1204 km^2. The mean annual temperature of Great Lake Saint-François watershed varies from 2.5 to 5.0 °C. The mean annual precipitation is about 1000 to 1100 mm, and the length of the growing season extends over 170 to 180 days. The region surrounding the lake is essentially (75%) forested with maple (*Acer saccharum* Marsh.), birch (*Betula alleghaniensis* Britt.) or fir (*Abies balsamea* (L.) Mill.). The remainder of the watershed is occupied by agricultural fields and small villages (Robitaille and Saucier, 1998).

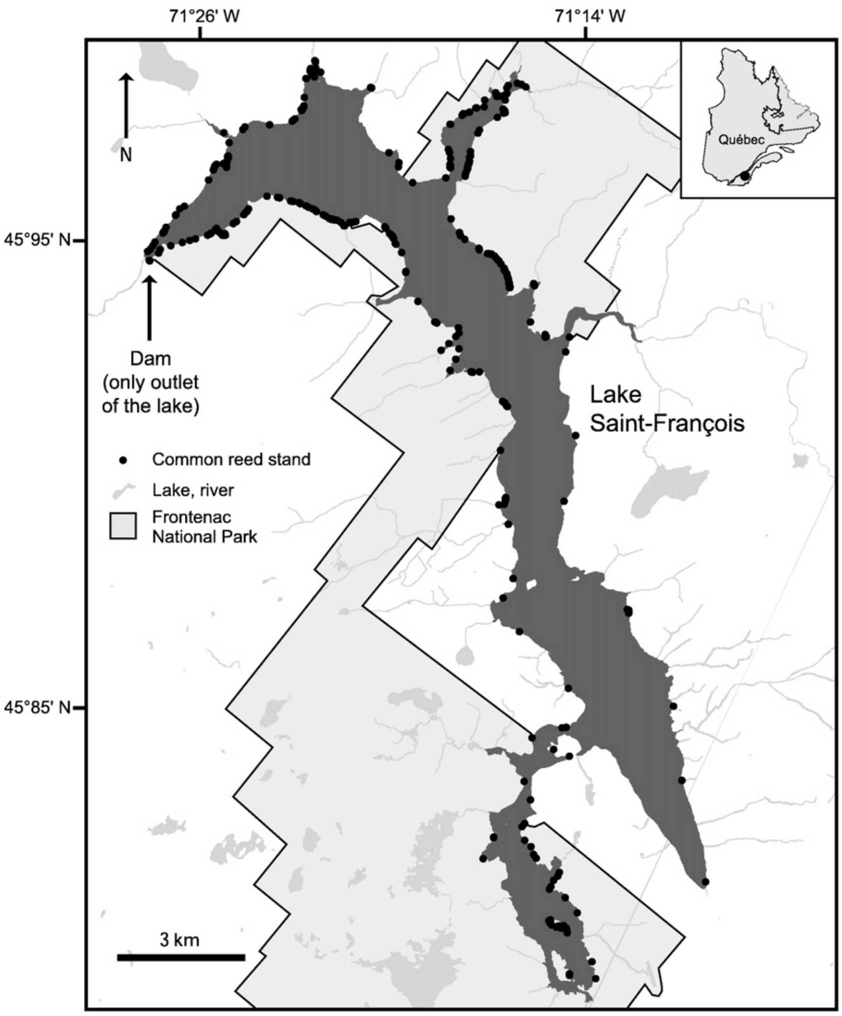

Fig. 1. Spatial distribution of common reed (*Phragmites australis*) populations on shores of Great Lake Saint-François (Québec, Canada) in summer 2006.

Great Lake Saint-François was dammed in 1917 for the production of hydroelectricity and to prevent spring floods. The water level is consequently highly variable (±8 m a year), and reaches its minimum level during the winter season. The mean water depth is 16 m, but the water depth may locally reach 40 m during the summer season (Ministère du Loisir, de la Chasse et de la Pêche du Québec, 1986). Approximately 63 of the 117 km of lakeshores are protected since 1987 within Frontenac National Park (Fig. 1), and have not recently been disturbed. The remaining 54 km are occupied by more than 900 residences. The forest vegetation (trees, shrubs) near these residences has in most cases been eliminated, and nearly all of their shores are now covered with rocks, concrete or lawn. Preliminary surveys conducted along shores protected by Frontenac National Park suggested that common reed stands, almost absent in 1995, were rapidly increasing in number and size (Société des établissements de plein air du Québec, 2005).

Sampling of common reed populations

Shores of the lake (inside and outside park) were visited with a small boat from July 24 to August 27, 2006, and all visually distinct common reed stands (i.e., a group of stems clearly isolated from its neighbours) were positioned with a geographic positioning system (GPS), mapped with a geographic information system (GIS), and measured (maximal extension parallel to the shore). A genetic study of these stands showed that they all belonged to the Eurasian subspecies (haplotype M) of common reed (Belzile et al., 2010). All roads surrounding Great Lake Saint-François (Fig. 2), over an area of 952 km^2, were also visited by car (July 17–21, 2006). The total length of the road system in this area was 615 km, including 177 km of regional roads (all paved) and 438 km of local roads (36% paved). Roads were never located more than 20 km from shores of Great Lake Saint-François. Each common reed population detected along roads was recorded with a GPS, and mapped with a GIS. The genotype of roadside stands was not validated by a genetic study, but recent studies on common reed populations located on roadsides in Québec showed that 95–99% of populations belong to the Eurasian subspecies (haplotype M) of common reed (Lelong et al., 2007; Jodoin et al., 2008).

Historical data on residential construction

Since the increasing number of residences located near lakeshores was suspected to have facilitated the recent invasion of Great Lake Saint-François by common reed, the history of the spatial distribution of residences was reconstructed (since 1930). Construction permits and assessment rolls from the five municipalities surrounding the lake were used to determine the year of construction of residences with a direct access to lakeshores. All residences with a known construction year were located on the field, positioned with a GPS, and mapped with a GIS.

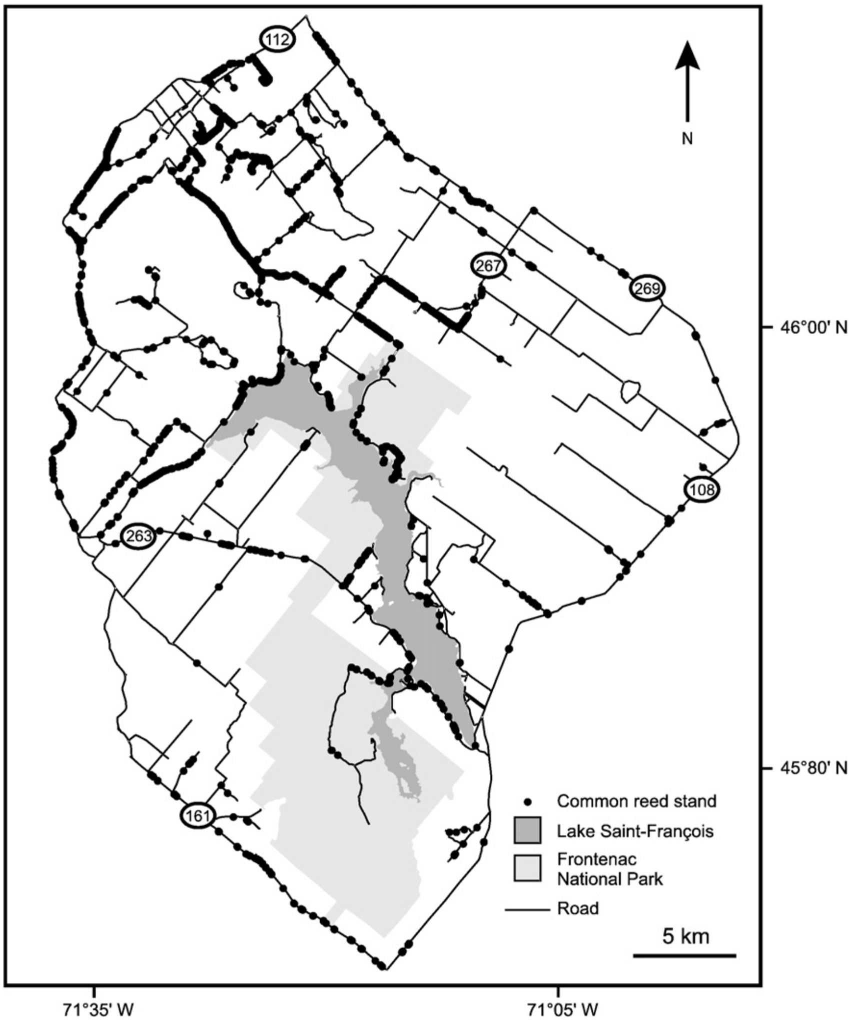

Fig. 2. Spatial distribution of common reed (*Phragmites australis*) populations along roads of Great Lake Saint-François region (Québec, Canada) in summer 2006. Regional roads are numbered (108, 112, 161, 263, 267 and 269).

Data generated with a geographic information system and statistical analyses

The clustering of common reed stands on shores of Great Lake Saint-François (Belzile et al., 2010) added an autocorrelation problem complicating the construction of a logistic regression model. To reduce autocorrelation, lakeshore was subdivided into 488 contiguous sections 250-m long. The length of a section was chosen to be much larger than the median length of a common reed stand (4.5 m; the maximum length of a stand was 89 m), while insuring a sufficient number of samples to build a robust logistic regression model considering the number of independent variables (Hosmer and Lemeshow, 2000; LeBlanc, 2008). The presence or absence of a common reed stand in a section was recorded as the dependent variable, regardless of the number of stands in the section.

Using a GIS and maps of the *Bases de données topographiques du Québec* (Ministère des Ressources naturelles et de la Faune du Québec, 2000), nine explanatory variables were measured and associated to each lakeshore section. Maps were used to identify the main land use (residential or forest; variable V1) along the lakeshore section, and the direction (facing N, S, E, W, NE, NW, SE or SW; V2) of the lakeshore; it was hypothesized that W, NW and SW sections would receive more wind or water-dispersed common reed diaspores, because located on the lee side. The GIS was used to measure the minimum distance separating the central point of each lakeshore section from the closest roadside common reed stand (V3), the closest road (paved or not; V4), and the closest paved road (V5). Paved roads, with their large and sunny roadsides, are usually bordered by more common reed stands than gravel roads (Lelong et al., 2009). The hypothesis tested was the smaller the distance between a paved road with a common reed population and the lakeshore, the higher the probability of the establishment of a common reed stand on this lakeshore. The GIS was also used to measure the minimum distance separating the central point of each lakeshore section from the closest tributary of the lake (V6), since these tributaries may function as corridors for the spread of common reed diaspores (Fér and Hroudová, 2009). Other distances that were measured were those separating a section from the dam of the lake (the only outlet draining the lake water; V7), from the closest residence (V8), and from the closest residence built between 1990 and 2006 (V9), i.e., the period during which common reed populations probably expanded along shores of Great Lake Saint-François.

Spatial, historical and land use factors that contributed to favour the presence of a common reed stand along shores of Great Lake Saint-François (the nine explanatory variables mentioned above) were identified with a binary logistic regression model (Hosmer and Lemeshow, 2000). The 488 lakeshore sections (250-m long) were used in the model. The SPSS software (SPSS Inc., 2004) was used for calculations.

Results

A total of 345 common reed stands were mapped along shores of Great Lake Saint-François (Fig. 1). They were especially abundant in the northern part of the lake. Numerous common reed stands were present on shores that are protected by Frontenac National Park. A total of 2914 common reed stands were mapped along the 615 km of roads that were surveyed, especially in the northern part of the study area (Fig. 2). More than 83% of common reed stands located on roadsides were found along paved roads, although paved roads represented only 54% of the total length of the road system. Common reed stands were especially abundant (50% of roadside populations) along regional roads (29% of the total length of the road system).

It was possible to determine the construction year of 519 of the 900 residences that were located near lakeshores in 2006. Very few residences were built in the 1930s and 1940s (Fig. 3). The first residential boom occurred from 1950 to 1980, but almost exclusively in the northern part of the lake (Fig. 4). The second residential boom occurred from 1990 to 2006, especially (but not exclusively: 68% of the total) in the southern part of the lake. More than 44% of the 519 residences for which it was possible to determine the construction year were built during this period. The non-built shores are today almost exclusively located inside limits of Frontenac National Park.

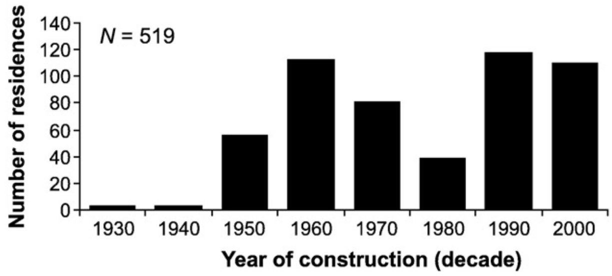

Fig. 3. Number of new residences with a direct access to shores of Great Lake Saint-François (Québec, Canada) built per decade. For the 2000s, data include only residences built from 2000 to 2006.

A common reed stand was present in 160 of the 488 lakeshore sections (250-m long) that were delineated. Only four of the nine independent variables that were used in the logistic regression model were significant (Table 1); 27% of the variance was explained by the model. The probability of finding a common reed stand on a shore of Great Lake Saint-François increases with the proximity of the outlet of the lake (dam), and of a paved road. On the other hand, this probability decreases with the proximity of a residence built between 1990 and 2006, and with the proximity of a tributary of the lake.

Discussion

Considering that common reed populations were almost absent on shores of Great Lake Saint-François in the mid-1990s, the spread of haplotype M along the lake (345 populations in 2006) was remarkably rapid. It is likely that haplotype M first spread along the road system (especially paved roads) of the lake's region. Once well established along roads (in fact, in roadside ditches) surrounding the lake, it was only a matter of time before seeds of the plant, which can be dispersed by water or wind up to 10 km (Fér and Hroudová, 2009), would germinate on suitable seedbeds near lakeshores (Belzile et al., 2010); established individuals would then increase in number using clonal (rhizome, stolon) growth (Hudon et al., 2005). The high abundance of roadside populations (high diaspore pressure) in the northern part of the study area (where the outlet of the lake is located), and the fact that the lake water is naturally drained toward the outlet, may explain the statistical link found between the presence of a common reed stand and the distance separating the stand from the outlet. On the other hand, there is no evidence that small tributaries act as conduits for diaspores of common reed in the particular context of Great Lake Saint-François. Some residents hypothesized that water level changes of Great Lake Saint-François are in part responsible for the invasion of lakeshores by common reed. However, this hypothesis has to be rejected, because the water level is high in spring, summer and fall, and low in winter, i.e., only from the beginning of December to the end of April (Centre d'expertise hydrique du Gouvernement du Québec, 2010). In other words, soils of lakeshores are not exposed by water level draw downs during the most propitious period for seed germination (spring) or clonal propagation (summer), and then cannot contribute to facilitate the spread of the plant (Brisson et al., 2008).

What is more intriguing is the fact that the probability of finding a common reed stand decreases with the proximity of a residence built

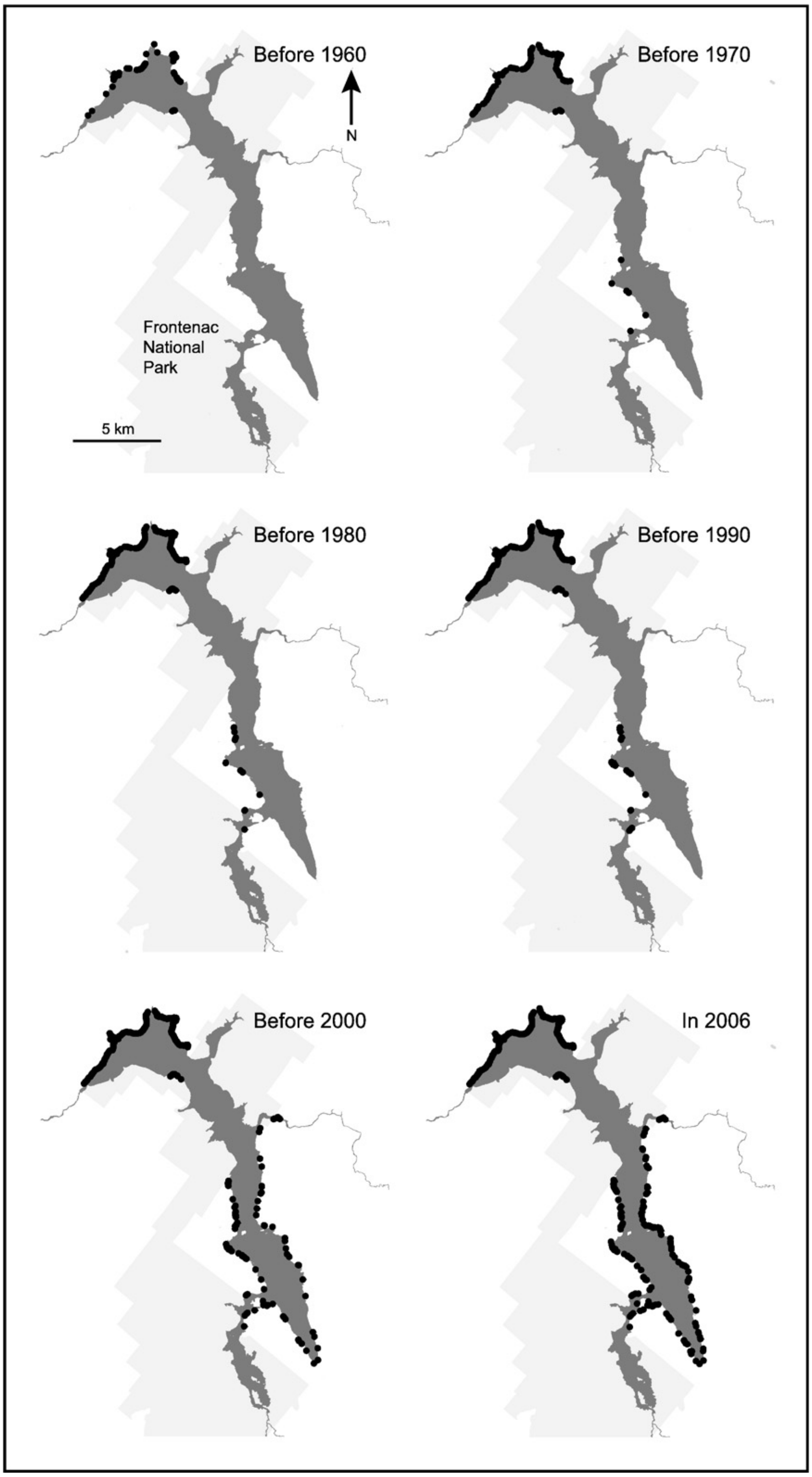

Fig. 4. Spatial distribution of residences (black dots) with a direct access to shores of Great Lake Saint-François (Québec, Canada) at different time periods.

between 1990 and 2006. Haplotype M of common reed is present in the study area since at least 1965 (Lelong et al., 2007), but the spread of the species along shores of Great Lake Saint-François was initiated only in the mid-1990s, i.e., a few years after the beginning of the second residential construction boom. There is some evidence that residential construction creates favourable seedbeds (bare soil) for common reed (Fig. 5); construction works can also contribute to the importation of soils containing diaspores. Seeds of this plant species germinate on moist soil or under 0–1 cm of water; germination is poor under vegetation and litter cover (Mal and Narine, 2004). However, the logistic regression model that has been constructed for this study does not support the hypothesis that residential construction facilitated the establishment of common reed stands.

A potential explanation for this incoherence is the fact that the residential construction boom of the 1990s and 2000s occurred essentially in the southern part of Great Lake Saint-François, where

Table 1
Results of the binary logistic regression model that has been used to establish a link between the presence of a common reed (*Phragmites australis*) population along the shores of the Great Lake Saint-François (Québec, Canada), and some environmental variables.

Significant variable	β	SE	Wald	P
Distance to the outlet of the lake	−0.015	0.002	39.342	<0.001
Distance to the closest residence built between 1990 and 2006	0.052	0.010	26.608	<0.001
Distance to the closest tributary of the lake	0.071	0.021	11.144	<0.001
Distance to the closest paved road	−0.019	0.007	7.172	0.007

the number of roadside common reed populations is much lower than in the northern part of the study area, hence resulting in less diaspore pressure. The southern part of the lake is also remote from the lake's outlet, where common reed diaspores probably concentrate. It is thus possible that although seedbeds (bare soils near lakeshores) were created in the southern part of the lake during the residential construction boom, common reed seed rain was not dense enough to be responsible for the establishment of a large number of populations of the plant. The residential boom was less intense in the northern part of the lake, but probably sufficient enough (a minimum of 73 residences) to trigger common reed invasion, considering the density of roadside common reed populations in the northern part of the study area. It is also noteworthy that in the northern part of the lake, a large number of common reed populations established on undisturbed lakeshores protected by Frontenac National Park. It may be hypothesized that in this part of the lake, the seed rain is so dense that even unlikely events—the establishment of common reed populations on undisturbed lakeshores—occur. The quantification of the seed rain (wind or water dispersed) would be nevertheless essential to test this hypothesis.

Common reed may have indirectly benefited from the residential construction boom of the 1990s and 2000s through nutrient enrichment of the lake's water (Bertness et al., 2002). Very few residences have conserved their original plant cover, and chemical fertilizers widely used to enrich lawns have contributed to pollute the water. Furthermore, there was recently an expansion of pig farms in Great Lake Saint-François watershed (+65% of the number of animals since 1991), and consequently of the spreading of pig manure on agricultural lands, which could have contributed to enrich with nitrogen and phosphorus the water of the tributaries of the lake (Guay et al., 2009). The multiplication of cyanobacteria blooms in the 2000s strongly suggests that there is a decrease in the water quality of this lake (R. Charest, Frontenac National Park, personal communication).

Whatever the exact role of residential construction on the spread of haplotype M of common reed, the recent invasion of Great Lake Saint-François shows that the spread of common reed in North America is not restricted to major river or road systems. Large or small lakes, if submitted to intense diaspore pressure, can also be at risk, even those located far inland. Disturbances on lakeshores can contribute directly or indirectly to the establishment of common reed, but even undisturbed sites can be colonized if seed rain is sufficient. Here, the presence of a road network acting as an invasion conduit combined with spatial constraints (the outlet) directing the movement of seeds explained early invasion patterns of common reed. Given the scale of recent disturbances on the lakeshore, it may be only a matter of time until lakeshores become even more invaded. We suspect that this phenomenon (lakes and rivers invaded by common reed) is much more widespread than actually known; it should be more thoroughly documented, to eventually develop prevention measures, such as the identification and eradication of potential invasion sources nearby sensitive areas, and the rapid revegetation of bare soils after construction activities.

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Fig. 5. Common reed population that has established on the shore of a residence (built in 2006) with a direct access to Great Lake Saint-François (Québec, Canada). The construction of this residence implied the removal of the vegetation covering the ground, which may have provided a suitable seedbed for the plant (photograph: Marie-Claire LeBlanc).

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