Introduction and transfer of alien aquatic species in the Great Lakes–St.Lawrence River drainage basin

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The introduction of and invasion of new territory by alien species has become a global problem threatening the diversity and integrity of ecosystems in all parts of the world (Carlton and Geller 1993; Cohen and Carlton 1998; Sala et al. 2000). Species introductions in aquatic systems are mainly caused by human activities, which have practically eliminated the natural geographic barriers to dispersion and gene flow of species across otherwise isolated drainage basins (Drake et al. 1989; Mills et al. 1993; Mills et al. 1997). With regard to biodiversity, the introduction of species leads to homogenization of the biota (Rahel 2000), and introduced species occasionally become the dominant life-forms in an ecosystem (Cohen and Carlton 1998; Galatowitsch et al. 1999).

In North American waters, the introduction of alien species began with European settlements and the associated development of economic activities. The first species introductions occurred through deliberate releases of imported plants and through stocking of fish (Dextrase and Coscarelli 1999). Alien species have received much attention over the past 15 years after the unintentional introduction, spread, and subsequent economic and ecological impacts of both zebra mussel (*Dreissena polymorpha* (Pallas)) and quagga mussel (*Dreissena bugensis*) (Nalepa and Schloesser 1993; Claudi and Mackie 1994). Ironically, in response to the increasing scientific and public awareness of the problem, the Great Lakes now represent one of the best, if not the best, documented aquatic systems with regard to alien species. For example, in their extensive review, Mills et al. (1993) listed 139 species introduced into the Great Lakes up to 1991.

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The Great Lakes–St. Lawrence River system (Figure 1) is the largest and most economically important drainage basin in Canada (Government of Canada 1991). However, this ecosystem has been severely impacted by human activities such as agriculture, shoreline development, urbanization, and industrialization (Shear 1996). Since the explorations of Jacques Cartier, who sailed the St. Lawrence River up to Montréal in 1535, many thousands of foreign and local vessels have traveled into the St. Lawrence–Great Lakes corridor, contributing to the region's economic development. To facilitate the trade of goods across the continent, the Great Lakes were artificially connected to the Hudson River drainage basin by the Erie Canal in 1825 and to the Illinois–Mississipi River drainage basin by the Chicago Canal at the southern end of Lake Michigan in 1848 (Mills et al. 1999). These environmental changes led to the introduction, and subsequent transfer, of various alien species (Mills et al. 1993; Mills et al. 1999; Wiley and Claudi 1999).

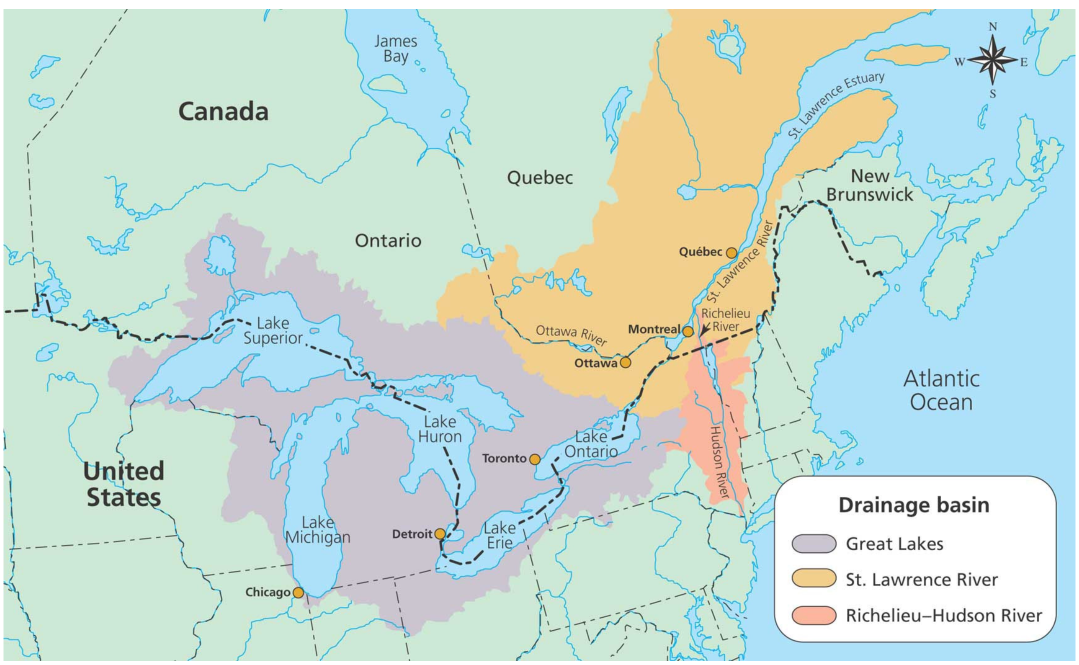

Figure 1. Map of the Great Lakes–St. Lawrence River drainage basin, with identification of major locations cited in the text.

Despite the natural link between the Great Lakes and the St. Lawrence River, very little is known about alien species in the St. Lawrence River. Because of its geographic position at the end of the drainage basin, the St. Lawrence River is the natural outflow of water from the Great Lakes and, as such, is continuously exposed to downstream transport of and colonization by organisms from upstream sources. The St. Lawrence River also represents the gateway for both local and foreign ships traveling into the Great Lakes. Between 1978 and 1996, the number of ships from foreign countries that went up the river as far as Montréal averaged 1050 per year, but only 250 vessels each year moved up into the Great Lakes to their first port of entry (Bourgeois et al. 2001). In terms of ballast capacity, the volume of water discharged into the St. Lawrence River is 4 times higher than that entering the Great Lakes. Montréal is by far the most important harbor in the system for foreign shipping, and each year it receives, on average, nearly 3 times more foreign vessels and ballast water than the entire Great Lakes system. Therefore, the St. Lawrence River is definitely subject to the introduction of alien species from outside the country, as well as to the transfer of organisms from upstream sources either by natural drift or assisted by ship transport. Equally, the St. Lawrence River may act as a potential source of alien species for the Great Lakes through upstream transfer by shipping or other assisted mechanisms. These scenarios are only hypotheses, as there has been no assessment of species transfer encompassing the whole drainage basin of the Great Lakes and the St. Lawrence River.

This chapter presents an overview of the current status of alien species in the Great Lakes–St. Lawrence River ecosystem, providing the first such assessment for the St. Lawrence River. It also evaluates the importance of downstream relative to upstream transfer of alien species between the Great Lakes and the St. Lawrence River. More precisely, this analysis has the following aims:

1. to list the species introduced and established in the Great Lakes and in the St. Lawrence River in the past 200 years,
2. to examine the relative proportion of introduced species now found in each region, and
3. to assess and compare the historic and present rate of species introductions in each region and thereby determine the extent to which the St. Lawrence River represents a potential source of alien species for the Great Lakes and other tributary drainage basins.

For convenience, our inventory follows that of Mills et al. (1993) in including only freshwater aquatic species and excluding strictly terrestrial plants and large vertebrates such as reptiles, birds, and mammals.

Data Collection

Data were obtained through an extensive search of various documents and other resources, including scientific papers, books, technical reports, computerized databases, and Web sites. For the St. Lawrence River, museum and herbarium collections were also examined. Relevant information on the presence, distribution, and abundance of alien species was compiled in a database. Data included the scientific and common names of the species, the date and site of introduction into the Great Lakes–St. Lawrence River drainage basin, the date and location of first report of the species in the St. Lawrence River (if present), the geographic origin of the species, and the identified vector of introduction. When in doubt, we consulted scientific experts to validate the data. Following the definition adopted by Mills et al. (1997), the date of introduction corresponds to the date of the first recorded release, observation, or collection. In the few cases where the date of first publication was the only information available, the date of introduction was identified as before (<) the date of publication. The vectors of introduction were grouped and coded as in Mills et al. (1993). Deliberate introduction was defined as that occurring through agriculture or fish-stocking activities, and unintentional introduction was defined as that occurring through aquarium releases, aquaculture escapes, bait release, ship fouling, ship ballast, or canals.

Alien Species in the Great Lakes–St. Lawrence Basin

A total of 163 species have been introduced in the entire Great Lakes–St. Lawrence River drainage basin (Table 1, Figure 2). These species belong to various taxonomic groups (algae, vascular plants, invertebrates, and fish), but alien amphibians have not been reported (Benson 1999). Of that total, 160 have been reported from the Great Lakes. This number includes an additional 21 new species since Mills et al. (1993): 13 invertebrate species, 6 fish species, 1 vascular plant, and 1 algal species. These new additions are identified by a plus sign (+) in Table

1. Of this group, 8 invertebrate species, 1 fish species, and the vascular plant were reported after 1990 and are considered recent introductions. One mollusk species (*Pisidium moitessierianum*), which was reported only recently, in 1997, was apparently introduced during the 19th century and might have been misidentified or confused with another species since then (Grigorovich et al. 2000). The remaining 10 species were reported before 1990 and were probably missed by Mills et al. (1993).

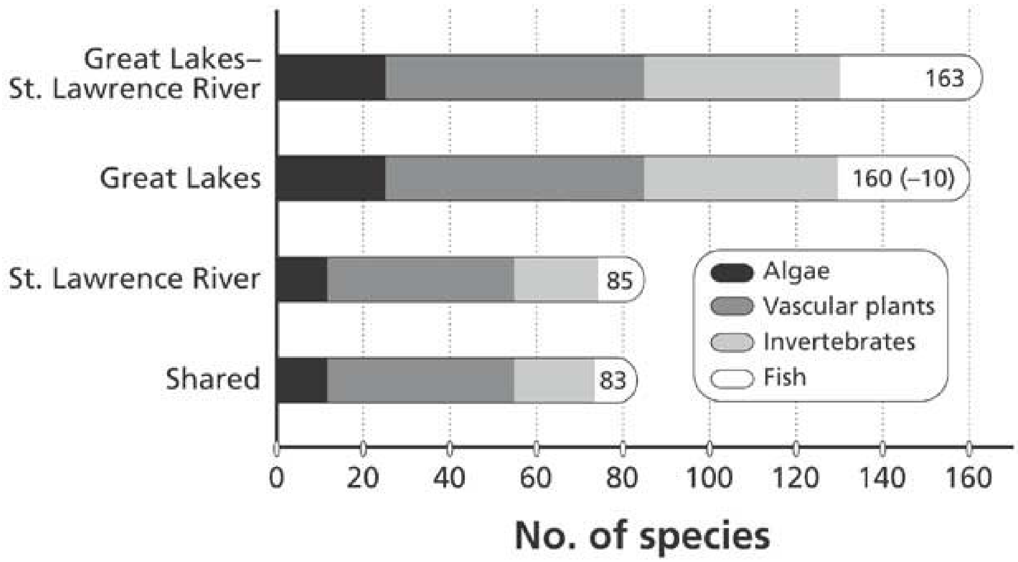

Figure 2. Number of alien species reported in the Great Lakes and in the St. Lawrence River drainage basin. Note that 10 species introduced into the Great Lakes are endemic to the St. Lawrence River.

Of the 160 species introduced into the Great Lakes, 10 are native to the St. Lawrence River and other rivers of the northeastern North American coast (Table 1). This group consists of 1 algal species, 1 invertebrate species, 2 vascular plants, and 6 fish species. Rainbow smelt (*Osmerus mordax* (Mitchill)) was deliberately introduced in the Lake Michigan system in 1912, but the introductions of the other species into the Great Lakes were due to shipping activities. Solid and liquid ballast releases are believed to have been responsible for the transfer of the single algal species (*Bangia atropurpurea*), one of the vascular plants (*Juncus gerardii*), the invertebrate (*Gammarus fasciatus*), and one fish species (*Apeltes quadratus* (Mitchill)). Ship canals are indicated as the source of entry for 4 fish species. The three-spined stickleback (*Gasterosteus aculeatus* L.) reached Lake Huron in 1980 via the artificial Nipissing Canal (Fuller et al. 1999), whereas alewife (*Alosa pseudoharengus* (Wilson)), white perch (*Morone americana* (Gmelin)), and sea lamprey (*Petromyzon marinus* L.), presumably invaded the Great Lakes via the Erie Canal (Mills et al. 1993). However, upstream migration of these species from the St. Lawrence River cannot be ruled out (Scott and Crossman 1973).

Given that these 10 species are native along the North American Atlantic coast, it is difficult to ascertain precisely whether they originated from the St. Lawrence River or from other sources. Studies on the population genetic structure of these species would provide further clues. In theory, native species would consist of several genetically distinct local populations, whereas introduced species would be characterized by less genetic variability. As a consequence, the analysis of genetic distance among populations of species introduced into the Great Lakes and those from sites within their native ranges in North America would identify the populations of origin and the routes of entry. For example, Hogg et al. (1999) recently compared the population structure of 2 species of amphipods within the Great Lakes–St. Lawrence River drainage basin. Their results showed much higher levels of genetic differentiation for the native amphipod *Hyalella azteca* than for the introduced species *Gammarus fasciatus* (from Lake Superior to Québec).

Eighty-seven alien species have been introduced into the St. Lawrence River and its tributaries. Eighty-five species have been observed in the St. Lawrence itself (Figure 2), and 2 species recently invaded the Richelieu River, a major tributary of the St. Lawrence. Overall, only 3 alien species currently found in the St. Lawrence River drainage basin have not yet been reported in the Great Lakes. These are the spinycheek crayfish (*Orconectes limosus*), the cutthroat trout (*Oncorhynchus clarki* (Richardson)), and the very recently introduced tench (*Tinca tinca* (L.)). The spinycheek crayfish was presumably introduced into the river in the late 1960s from southern New York via the Lake Champlain–Richelieu River waterways. It is uncertain whether these relatively new records are the result of natural expansion or unintentional introductions (Hamr 1998). This intruder is abundant in the downstream sector of the St. Lawrence River, where it has displaced and almost eliminated the native crayfish *Orconectes virilis* (Jean Dubé, pers. comm.). Sampling surveys conducted during summer 2000 confirmed that *O. limosus* is the dominant crayfish downstream of Montréal but is very rare upstream, where *O. virilis* is still common (de Lafontaine, unpublished data). The presence of cutthroat trout in the St. Lawrence is the result of fish stocking that took place in some tributaries along the north shore of the river in the 1940s.

The introduction of tench into the upper Richelieu River was confirmed in October 1999 from specimens captured in commercial fisheries (Dumont et al. 2001). The species had escaped from fish farming ponds in 1991, following its unauthorized import from Germany in 1986. Although introduced and established in many states of the United States (Fuller et al. 1999), this is only the second record of tench in Canadian waters, the first being from British Columbia lakes (Dumont et al. 2001). Given the highly invasive character of this species, it is expected that tench will eventually move downstream into the St. Lawrence River. Similarly, the invasive water chestnut (*Trapa natans*) was reported in the upper Richelieu River for the first time in 1998 (Gratton 1998). The source of introduction is unknown but was probably an accidental transfer by pleasure boats and trailers, a release from cultivation, or an input from southern Lake Champlain and New York populations (Ann Bove, pers. comm.). Unless it is rapidly eradicated, the species will spread further downstream along the Richelieu River and eventually invade the shoreline habitats and wetlands of the St. Lawrence River. Although water chestnut has been observed at some locations around the Great Lakes (Mills et al. 1993), it is still absent from the St. Lawrence River.

A total of 83 alien species occur in both the Great Lakes and the St. Lawrence River (Figure 2). About 55% (83 of 150) of the species introduced into the Great Lakes and not originally present in the St. Lawrence River have now been reported from the river. Although the number of introduced species in the Great Lakes is twice that for the St. Lawrence River, the relative proportion of the various taxonomic groups differs between the 2 systems. There are between 2.0 and 2.3 times more invertebrate, fish, and algal species, but only 1.3 times more vascular plant species in the Great Lakes. Alien vascular plant species are more numerous in the St. Lawrence River (51%) than in the Great Lakes (38%).

The alien species common to the Great Lakes and the St. Lawrence River are not from the same geographic origins as those found only in the St. Lawrence River (Table 2). Species from Eurasia dominate in the river (66%), whereas they account for only half (47%) of the species in the entire basin. Conversely, the number of species from the Atlantic coast, the Mississippi River basin, and Asia are proportionally higher in the Great Lakes than in the river.

Rate of Species Introduction and Transfer

The number of alien species introductions over time follows different patterns in the Great Lakes and the St. Lawrence River (Figure 3). In the Great Lakes, the numbers of species introduced in 20-year periods gradually increased after 1820, levelling off at about 20 to 25 species every 2 decades since 1921 (Mills et al. 1993). This translates to an average rate of introduction of about one species per year. Plant introductions dominated in the early years, with some invertebrate and fish introductions reported in the late 1800s. Introductions peaked during the period from 1961 to 1980 because of the numerous reports of new algae. During the past 20 years, 21 new species, mostly invertebrates (12) and fish (7), have been introduced.

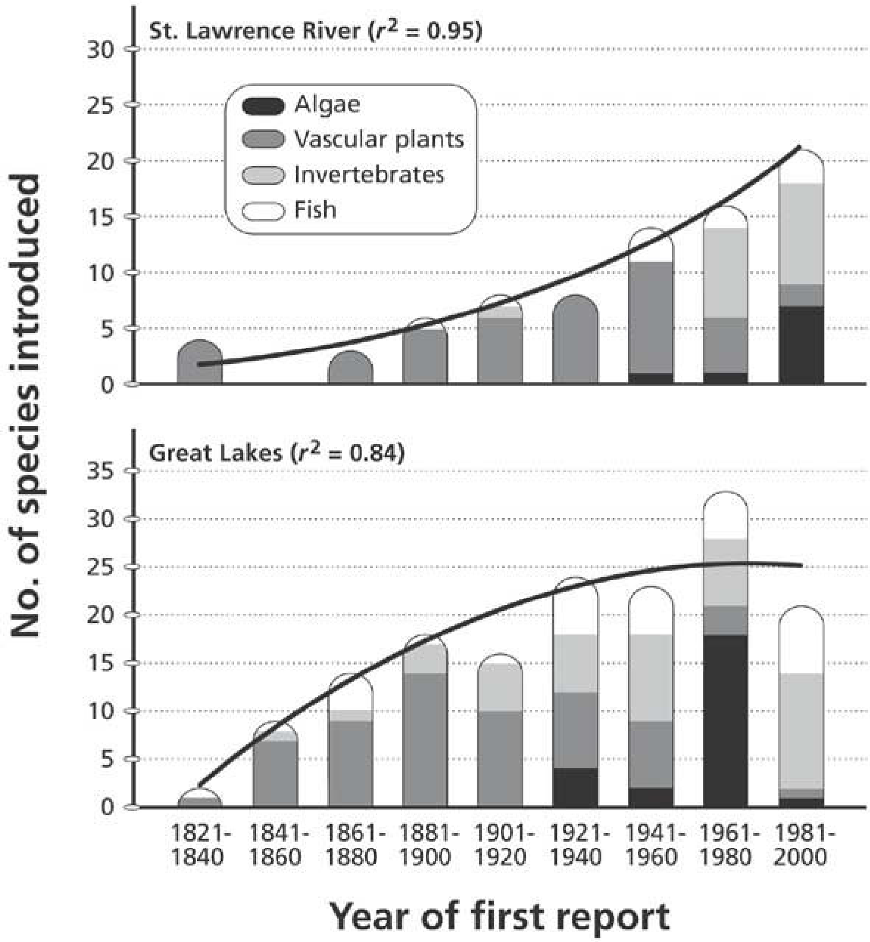

Figure 3. Temporal succession of species introductions in the St. Lawrence River and the Great Lakes, sorted by taxonomic groups.

In contrast, since 1820, species introductions in the St. Lawrence River have increased almost exponentially (Figure 3). Introductions peaked during the last 20-year period (1980–2000), with a total of 21 new species recorded. This is similar to that observed in the Great Lakes. Up until 1960, introduced species were mainly vascular plants, but since then reported species have been mostly invertebrates.

Comparison of the dates of introduction for the species common to the 2 regions reveals that 65 (83%) of the 78 species with known dates of introduction were reported in the Great Lakes before being found in the St. Lawrence River. This pattern suggests downstream transfer via either natural or anthropogenic dispersal. For each species, the time required for transfer was estimated by calculating the difference (in years) between the date of the first report from the Great Lakes and that from the St. Lawrence River (Table 1). Values vary greatly among and between taxonomic groups (Table 3). On average, downstream transfer has been most rapid for algae (mean 31.5 years, median 21 years) and slowest for vascular plants (mean 52.0 years, median 56 years). Transfer of fish and invertebrates has usually been slow, averaging 40 years. These average estimates are based solely on species common to the 2 regions and do not account for the temporal variation in the proportion of species in each group that have reached the St. Lawrence River. The proportion of species first observed in the Great Lakes and later reported in the St. Lawrence River has decreased with time (Figure 4). Nearly all species that were introduced more than 100 years ago have been transferred and reported in the river. Only 10% to 35% of the species introduced during the past 40 years had been reported in the river by 2000. The pattern is relatively independent of taxonomic groups.

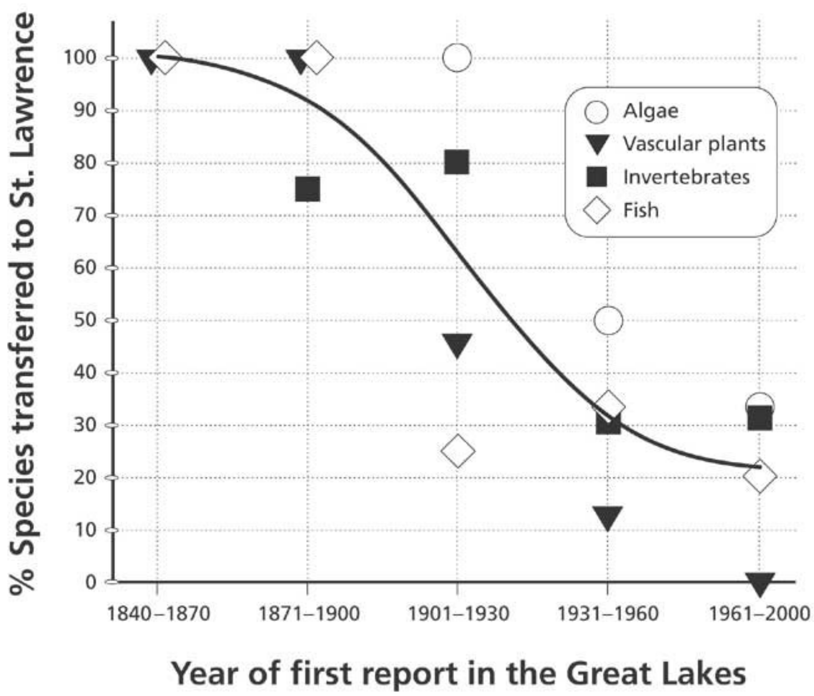

Figure 4. Proportion of species transferred from the Great Lakes into the St. Lawrence River as a function of year of first report in the Great Lakes.

Conversely, 13 species were discovered in the St. Lawrence River before being observed in the Great Lakes. This suggests some upstream transfer of species between the river and the lakes. Twelve vascular plants were introduced in the late 1800s and early 1900s and one alga

(*Nitellopsis obtuse*) was first discovered in the river in 1978. The calculated upstream transfer time for vascular plants was 25 years (median 15 years). Adding the 2 species (spinycheek crayfish and cutthroat trout) present only in the St. Lawrence River yields a total of 15 alien species (out of 152 [10%]) first reported in the St. Lawrence River. For these species, the river might have been the first site of introduction in the Great Lakes–St. Lawrence River drainage basin or even in North America.

The majority of alien species introduced into the Great Lakes were first reported in Lake Ontario (n = 46), Lake Erie (n = 38), and Lake Michigan (n = 23). This is not surprising, given that these 3 lakes have been, and still are, subject to many more human activities and much more anthropogenic stress than the others. Important harbor facilities accommodating maritime traffic and large cargo ships are located on these lakes. The list of alien species in the St. Lawrence River is dominated by species first introduced into Lake Ontario (42%) followed by those first introduced into Lake Erie (27%) (Figure 5). This differs from the pattern observed for species found only in the Great Lakes, which is characterized by a relatively high proportion of species first introduced into Lake Erie and Lake Michigan. Species introduced into Lake Michigan are largely underrepresented in the St. Lawrence River.

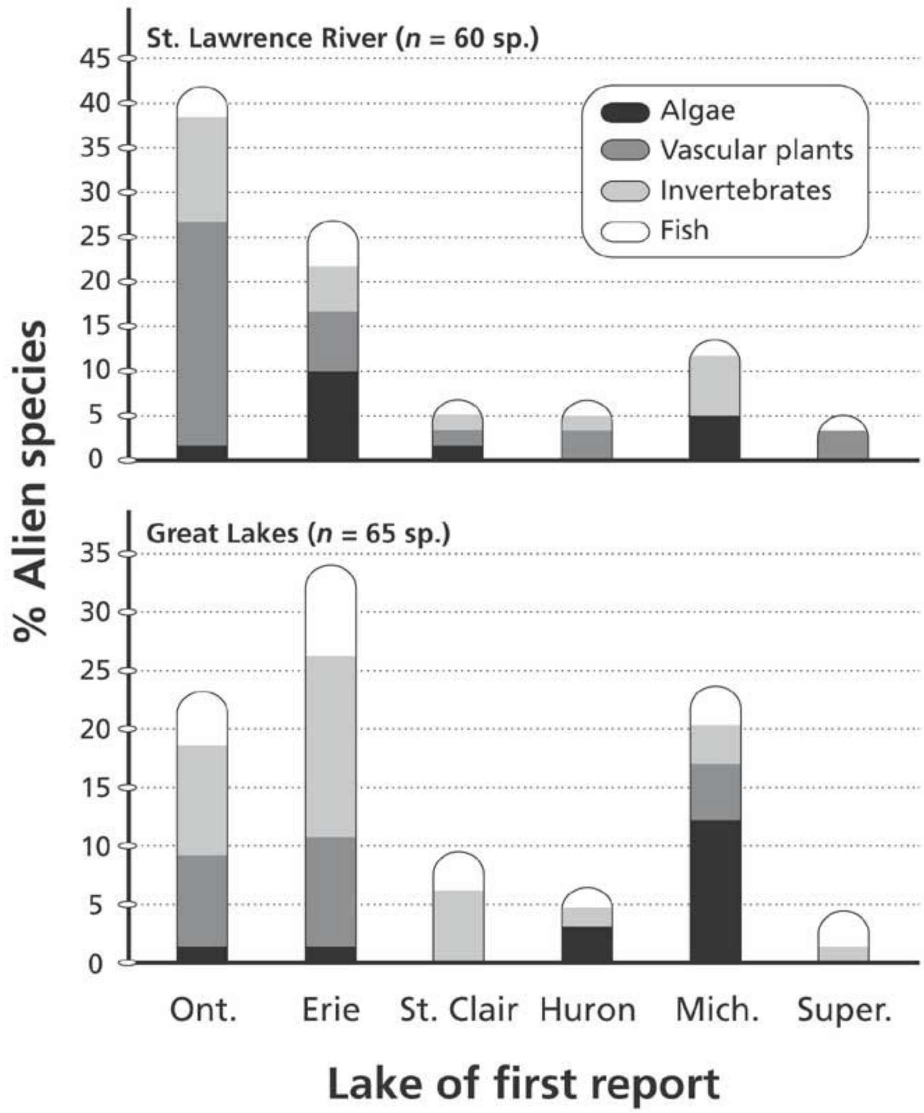

Figure 5. Relative proportion of alien species found in the St. Lawrence River (top panel) and in the Great Lakes only (bottom panel) as a function of the lake of first introduction. Super. = Superior; Mich. = Michigan; Ont. = Ontario.

Spatial Distribution of Alien Species in the St. Lawrence River

A complete description of the spatial distribution and relative abundance of alien species in the St. Lawrence River is beyond the scope of this chapter. Evidence of the spatial distribution of alien species along the St. Lawrence River was determined by compiling information on the presence and reports of each species (irrespective of abundance) in 13 arbitrarily defined sectors between Cornwall, Ontario, and the saltwater edge near Montmagny, Quebec, downstream of Québec. Half of the species (42 of 83 [50.6%]) have been observed in fewer than a quarter of the sectors, and only one-third (26 of 83 [31%]) have been reported in more than half of the sectors. The most widely distributed species are the diatom *Stephanodiscus binderanus*, 14 vascular plants (including purple loosestrife, *Lythrum salicaria*, and flowering rush, *Butomus ombellatus*), 3 invertebrates (the faucet snail, *Bithynia tentaculata*; the zebra mussel; and the quagga mussel), and 5 fish species (including common carp, *Cyprinus carpio* L.; the rainbow trout, *Oncorhynchus mykiss* (Walbaum); and the brown trout, *Salmo trutta* L.). Given the dynamic flow regime and the relatively short length of the river (about 300 km), the level of spatial heterogeneity for the alien species along the river is surprising. Two factors may contribute to this apparent patchiness. First, the high diversity of habitats along the river may help to maintain some level of spatial heterogeneity in the distribution of various species for which life-history characteristics and habitat requirements differ. Second, many introduced species may occur at very low densities in the river and are therefore not frequently encountered or sampled. Data for most species are too scant at present to adequately evaluate these possibilities.

Studies to quantify the ecological effect of alien species have generally dealt with specific cases of invasion (mostly for the Great Lakes), but the global impact of alien species on the Great Lakes–St. Lawrence ecosystem has been relatively more difficult to assess (Claudi and Leach 1999). With the exception of a study of the impact of zebra mussels on native unionid mussels (Ricciardi et al. 1996), little has been done to assess the relative impact of alien species in the St. Lawrence River. River and lake ecosystems are very different in their structure and function, so it would not be legitimate to extrapolate and apply the results of lake studies to the St. Lawrence River. The ratio of alien to native species can provide a basic index of the potential impact of introduced species on the biodiversity of a system (Gido and Brown 1999; Whittier and Kincaid 1999; Prieur-Richard and Lavorel 2000; Rahel 2000). Such an index, based on species richness, has been particularly useful for documenting the effect of alien species in terrestrial plant communities, but not aquatic systems. The index requires an intensive and detailed inventory of both alien and native species, which may represent an enormous and often tedious task for some aquatic communities (e.g., benthic or planktonic communities).

According to the most recent and very extensive account of the St. Lawrence river phytoplankton by Paquet et al. (1998), [who reported 364 taxa, the number of introduced algae (*n* = 12; see Table 1) represents only 3% of the overall phytoplanktonic community. Hall and Mills (2000) reported that alien fish species represented between 11% and 17% of the fish species richness in each of the 5 Great Lakes. Given an estimated total number of 93 fish species in the St. Lawrence River (Bernatchez and Giroux 1996), the relative proportion of alien fish species (*n* = 11; see Table 1) is 12%, similar to that reported for the Great Lakes. However, these estimates are less than those calculated for small northeastern lakes, where the proportion of alien species often exceeded 25% of the overall fish assemblage (Whittier and Kincaid 1999).

To further estimate fishery impacts in the St. Lawrence River, fish catch data collected daily since 1971 at the experimental trap fishery of the Aquarium du Québec, located at Saint-Nicolas, near Québec, were examined. Given that the alien fishes present in the river were introduced a long time ago (Table 1), an attempt was made to assess their relative importance to the structure and diversity of the fish community in the St. Lawrence River. In terms of species richness, alien species accounted for 7% to 14% (mean 10%) of the total number of species (40–48 species) captured at the experimental trap with no significant trend over the past 30 years (Figure 6). The percentage of alien fish in the total catch was, however, more variable, and exhibited 3 definite peaks, reaching up to 22%. No temporal trend was evident, and the peaks in relative abundance are indicative of the level of variability in recruitment and population dynamics of these alien species. Common carp (first observed in the river in 1908) and gizzard shad (*Dorosoma cepedianum* (Lesueur), first reported in 1944) are the 2 numerically dominant alien fish species in that fishery, but the proportion of introduced salmonids has increased over time. This increase is attributed to recent stocking programs in several lakes and tributaries within the St. Lawrence River drainage basin (Dumont et al. 1988). The present situation with regard to alien fish species in the St. Lawrence River may change dramatically in the near future with the introduction of the round goby (*Neogobius melanostomus* (Pallas)) into the St. Lawrence River. Downstream extension of the Great Lakes distribution of the goby is expected (Table 1). First reported in fall 1997 at a commercial trap fishery near Quebec City, the species was reported again on the south shore of Lake St. François (near Massena, New York) and at Saint-Nicolas in 2000. Our results further suggest that species richness is not sufficient to describe the potential impact of alien species in an ecosystem; an index based on relative abundance or biomass of alien relative to native species should also be used to determine ecosystem properties and responses to species introductions.

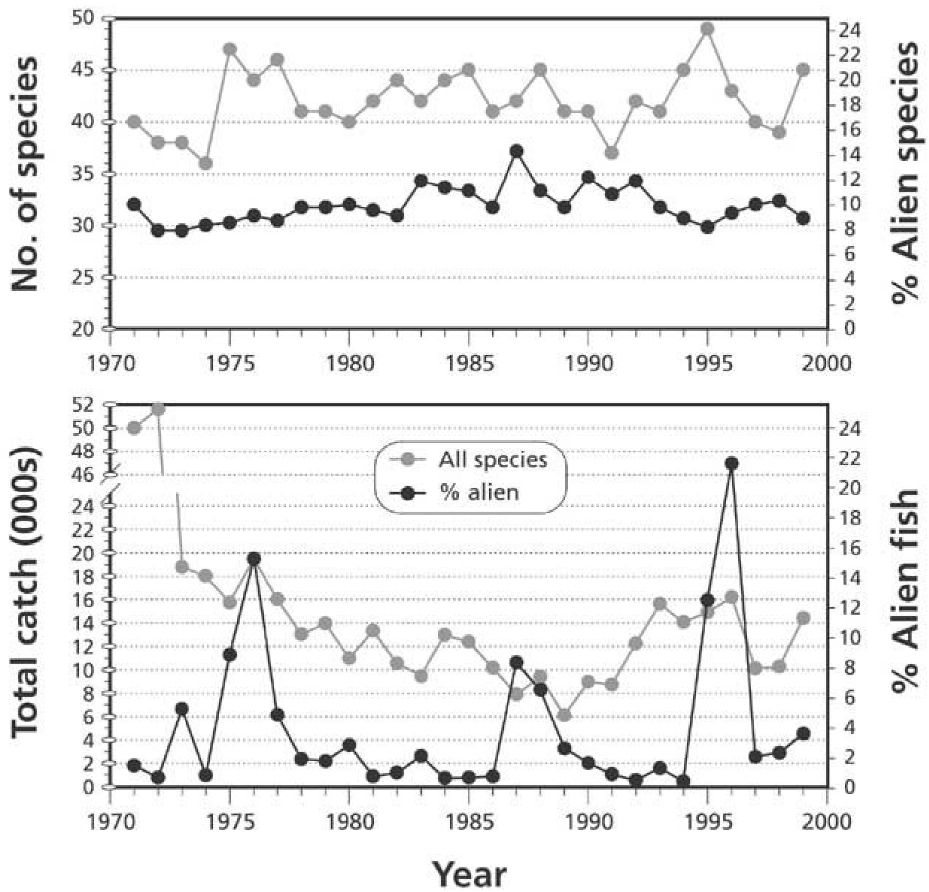

Figure 6. Relative importance of alien fish species in the fish community of the St. Lawrence River at Saint-Nicolas between 1971 and 1999.

Discussion

The count of 163 alien species in the entire Great Lakes–St. Lawrence River drainage basin is considered a conservative estimate, as the list (Table 1) is certainly not complete. As pointed out by Benson (1999), introductions of small organisms and those for which taxonomic classification is difficult have received much less attention and are less well documented. In fresh waters, taxonomic difficulties are particularly important for planktonic organisms, bryozoans, benthic worms, parasites, fungi, and other pathogens. Introduced species can carry cryptic species, which may not be easily recognized by nonexperts (Carlton 1999; Grigorovich et al. 2000). They can also act as disease vectors for some native species (see examples cited in Dextrase and Coscarelli 1999; Goodchild 1999). A notable example is the introduction of the spinycheek crayfish, *O. limosus*, to Europe, where it decimated native crayfish populations through the transfer of a pathogenic fungus (Lodge et al. 2000). Although these factors may impede the capacity to detect new species within these numerically abundant groups, it will not be surprising if, in the future, other alien species are added to the current list as a result of improved diagnostic and identification methods.

The rate of species introductions in the Great Lakes has been approximately one per year since 1920. The lack of similar indexes for other aquatic systems precludes any comparison, but intuitively this value would exceed by far the rate of species expansion due to natural causes. It should therefore be considered indicative of a serious problem. The slightly lower number of new alien species reported during the past 10 years (Table 4) tends to confirm a decline in species introductions, as anticipated by Mills et al. (1993). Transport by ships and through canals has been identified as a major vector of introductions into the Great Lakes (Locke et al. 1993; Wiley 1997; Wiley and Claudi 1999) and is implicated as a primary or secondary cause of introductions for nearly half of the species (Table 1). The significant increase in the number of introduced species during the 20th century was primarily a result of the change from solid ballast to water ballast in cargo ships and, probably more importantly, the opening of the Great Lakes–St. Lawrence Seaway in 1959 (Mills et al. 1993; Mills et al. 1999). The latter event would have caused the peak in species introductions between 1960 and 1980. It is worth noting that this peak was largely due to the reporting of 18 new algal species and coincided with the period of high eutrophication in the Great Lakes (Government of Canada 1991). This environmental crisis has contributed to scientific interest and led to increased sampling effort for phytoplankton and algae, which may have favored the discovery and identification of new species.

Guidelines for regulating the ballast discharged by ships entering the fresh waters of the Great Lakes–St. Lawrence River ecosystem were put forward by the Canadian government in 1989 (Wiley and Claudi 1999) in response to the severe impacts of zebra mussel introductions in the mid-1980s and in an attempt to reduce the number of species introductions by this means. The rate of compliance with these guidelines exceeded 90% after 1993 (Wiley 1995). It is interesting to note that the number of new species reported in the Great Lakes during the decade 1991–2000 (9 species) is the lowest for a 10-year period since 1920 (Table 4). Species introductions attributed to ships' ballast over the past 10 years have also dropped, to 5 from the 9 or 10 per 10-year period between 1960 and 1990. Although we do not maintain that the establishment of guidelines for ballast control have effectively contributed to the recent reduction in species introductions into the Great Lakes, these results tend to support the view that these guidelines for ships' ballast control, along with other control methods, may help to minimize the risk of new introductions of alien species into Canadian waters. Consequently, guidelines for ballast water exchange should be rigorously enforced along the St. Lawrence River.

More than half of the species that were introduced into the Great Lakes have been reported in the St. Lawrence River to date. In comparison, the Hudson River has more alien species (n = 113) than the St. Lawrence River but shares a lower percentage of species with the Great Lakes (48 [34%] of 139) (Mills et al. 1996). This indicates that the strategic position of the St. Lawrence River, the downstream end of the Great Lakes continuum, favors exchange and transfer of organisms, which in turn results in similarity of introduced species between the 2 regions. The majority (90%) of species introduced into the St. Lawrence River were first introduced into the Great Lakes, particularly Lake Ontario (Figure 5). Irrespective of the mechanisms involved, the St. Lawrence River appears to be highly exposed and vulnerable to downstream transfer and invasion by alien species introduced into the Great Lakes.

The introduction and the presence of alien species in the river does not necessarily imply the existence of established or self-perpetuating populations. As shown for zebra mussels in the Rhine River (Kern et al. 1994), river populations may be entirely dependent on annual recruits from reproducing populations in upstream lakes. A similar conclusion was reached by de

Lafontaine et al. (1995) and by de Lafontaine and Cusson (1997), who observed that zebra mussel larvae in the St. Lawrence River may have drifted from reproductive sources located as far as 250 to 500 km upstream in Lake Ontario. Comparative studies of the population dynamics of alien species in lakes and rivers would be very useful to determine the extent to which similar mechanisms exist for the alien species in the St. Lawrence River.

Our results suggest that the river may represent a potential source of entry for alien species in Canada and North America. Approximately 10% of the alien species reported in the Great Lakes were first found in and reported from the St. Lawrence River. Species first recorded from the river were vascular plants, introduced in the 1800s as the result of cultivation release or the discharge of solid ballast (Mills et al. 1994) in harbors of the St. Lawrence River. Although the contribution of the river as a primary receiving system for alien species seems to have been more important in the past, it is not negligible and it represents an active potential source of new introductions. The upstream transfer of these species, against the natural direction of water flow, implies that active or human-assisted mechanisms are responsible. Both foreign and domestic shipping activities are considered the most probable vectors for such transport (Niimi 2000). Similar upstream transfer of organisms (e.g., the zebra mussel, the round goby) within the Great Lakes has also occurred, as numerous species first introduced in the lower Great Lakes (Lake Ontario and Lake Erie) have spread into the upper lakes within a relatively short time (Wiley and Claudi 1999). These lines of evidence call for the development and implementation of adequate controls to reduce the active transfer of organisms within the drainage basin.

In theory, the likelihood that a species will be successfully transferred increases with time. Indeed, this analysis suggests that species transfer within the Great Lakes–St. Lawrence drainage basin is primarily a function of time elapsed since the first sighting (Figure 4) and distance from the original site of entry (Figure 5). The finding that the proportion of species common to both the lakes and the river increases with time since the first report implies that, once introduced, species will eventually spread and be distributed within the entire drainage basin. The results indicating that geographic distance influences the probability of species transfer within the basin (Figure 5) support the hypothesis that species may invade and establish themselves in communicating adjacent waters more rapidly and more successfully than in more distant locations (Johnson and Carlton 1996). Given that 62 species introduced into the Great Lakes have not yet been reported in the river, it is expected that the number of alien species reported in the St. Lawrence River will continue to increase in the near future. The exponential trend in species introductions in the river may well be maintained for another decade. In addition, species may also invade the St. Lawrence River from the river tributaries. The Richelieu River, which connects to Lake Champlain and the Hudson River drainage basin, has been identified as a source of species alien to the St. Lawrence River (e.g., the spinycheek crayfish) and may well be the route for future invasions by the tench and water chestnut, which have recently become established in its upper reaches.

Implications for Management

The above analysis depends entirely on the nature and the quality of the information available. To a large extent, this information is a function of the research efforts and number of studies conducted in a given region. If the probability of introducing a species is considered ecological roulette (sensu Carlton and Geller 1993), the discovery and confirmation of a new species is a matter of chance and sampling effort. Despite the fact that the introduction reports used to develop the present report originated from many different sources representing various levels of expertise, the proportion of species transferred over time, and transfer time estimates, were relatively similar among the various taxonomic groups. The reasons for this similarity are not obvious, but it would suggest that differences in transfer mechanisms between taxonomic groups are less important than the hydrological, ecological, and anthropogenic forces assisting the dispersion of organisms, within the Great Lakes–St. Lawrence River drainage basin in particular. With species introductions being essentially a human-related activity, it is not surprising that first reports of alien species were often from the areas of greatest anthropogenic impact, such as Lake Ontario, Lake Erie, and Lake Michigan (Figure 5). As a consequence, large harbor areas and canals would represent priority monitoring sites for species introductions and transfer in the Great Lakes and St. Lawrence River. Given the number of introductions associated with disposal of live bait (Litvak and Mandrak 1999), important fishing sectors permitting the use of live bait also warrant inspection and monitoring.

The spread of alien species throughout the Great Lakes and the St. Lawrence River has been relatively well described, and monitoring is already in place for a few species. Overall, however, very little information is available on the distribution and relative abundance of the vast majority of alien species. The lack of adequate monitoring programs for freshwater biodiversity in Canada is largely responsible for this situation. Such information is a prerequisite to assessing the relative importance, and the eventual impact, of alien species on Canadian ecosystems. Information systems in the United States (Benson 1999) and elsewhere (Ricciardi et al. 2000) have proven useful for compiling and synthesizing information (e.g., Fuller et al. 1999; Galatowitsch et al. 1999; Gido and Brown 1999; Rahel 2000).

Attempts to control and manage the problem at the species level may look promising, but the problem calls for a more holistic approach. Programs for chemical control of sea lamprey in the Great Lakes have resulted in enormous costs and effort over the last 50 years, and millions of dollars will continue to be spent in the future (Mills et al. 1999). Despite the harvesting programs developed to counteract the northward progression of water chesnut in Lake Champlain (Hauser and Bove 1999), the species has found its way into the Richelieu River (Gratton 1998), where it is now expanding rapidly. Shifting away from species management, effort and legislation to manage the human activities that contribute to species dispersal and transfer should be enhanced and strongly supported. Emphasis should be placed on the vectors of introduction, and the arbitrary distinction between deliberate and accidental introductions should be dismissed.

The dynamic and open nature of aquatic systems, as well as their natural continuity within a drainage basin, allows species to distribute widely within a given system. In recent years much emphasis has been dedicated to the introduction of species, but much less attention has been given to their subsequent transfer. The present analysis of the Great Lakes–St. Lawrence River basin reveals that these 2 aspects of the problem are equally important.

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Table 1. List of alien species introduced into the Great Lakes and the St. Lawrence River. The reported date of introduction is given for each region and the site of first report is given for the Great Lakes.

Taxon	Species	Family	Origin	Vector*	Great Lakes		St. Lawrence R
					Date	Site**	Date
Algae	*Actinocyclus normanii form subsalsa*	Bacillariophyceae	Northern Europe	S(BW)	1938	LO	
	Biddulphia laevis	Bacillariophyceae	Africa	S(BW)	1978	LM	
	Chaetoceros hohnii	Bacillariophyceae	Unknown	S(BW)	1978	LH	
	Cyclotella atomus	Bacillariophyceae	Widespread	S(BW)	1964	LM	
	Cyclotella cryptica	Bacillariophyceae	Widespread	S(BW)	1964	LM	
	Cyclotella pseudostelligera	Bacillariophyceae	Widespread	S(BW)	1946	LM	<1998
	Cyclotella woltereki	Bacillariophyceae	Widespread	S(BW)	1964	LM	
	Diatoma ehrenbergii	Bacillariophyceae	Widespread	S(BW)	1937	LM	Unknown
	Skeletonema potamos	Bacillariophyceae	Widespread	S(BW)	1963	LE	1996
	Skeletonema subsalsum	Bacillariophyceae	Baltic sea	S(BW)	1973	LE	1995
	Stephanodiscus binderanus	Bacillariophyceae	Eurasia	S(BW)	1938	LM	1955
	Stephanodiscus subtilis	Bacillariophyceae	Eurasia	S(BW)	1946	LM	
	+ *Terpsinoe musica*	Bacillariophyceae	Unknown	Unknown	1978	LM	
	Thalissiosira guillardii	Bacillariophyceae	Widespread	S(BW)	1973	LE	Unknown
	Thalissiosira lacustris	Bacillariophyceae	Widespread	S(BW)	<1978	LE	
	Thalissiosira pseudonana	Bacillariophyceae	Widespread	S(BW)	1973	LE	1994
	Thalissiosira weissflogii	Bacillariophyceae	Widespread	S(BW)	1962	LE	Unknown
	Enteromorpha intestinalis	Chlorophyceae	Atlantic	R(A)	1926	LO	1995
	Enteromorpha prolifera	Chlorophyceae	Atlantic	Unknown	1979	LSC	1999
	Nitellopsis obtusa	Chlorophyceae	Eurasia	S(BW)	1983	LSC	1978
	Hymenomonas roseola	Chrysophyceae	Eurasia	S(BW)	1975	LH	
	Bangia atropurpurea	Rhodophyceae	Atlantic N. coast	S(BW),S(F)	1964	LE	IND
	Chroodactylon ramosus	Rhodophyceae	Atlantic	S(BW)	1964	LE	<1982
	Sphacelaria fluviatilis	Sphacelariaceae	Asia	S(BW)	1975	LM	
	Sphacelaria lacustris	Sphacelariaceae	Unknown	S(BW)	1975	LM	
Plants	*Conium maculatum*	Apiaceae	Eurasia	R(C)	<1843		1832
	+ *Pistia stratiotes*	Araceae	South-east US	R(C)	2000	LE	
	Cirsium palustre	Asteraceae	Eurasia	Unknown	<1950	LS	1821
	Pluchea odorata var. purpurescens	Asteraceae	Atlantic	R(A)	1916	LE	
	Pluchea odorata var. succulenta	Asteraceae	Atlantic	Unknown	<1950	LO	
	Solidago sempervirens	Asteraceae	Atlantic	R(A)	1969	LM	IND
	Sonchus arvensis	Asteraceae	Eurasia	R(A)	1865	LO	1862
	Sonchus arvensis var. glaberescens	Asteraceae	Eurasia	R(A)	1902	LE	
	Impatiens glandulifera	Balsaminaceae	Asia	R(C)	1912	LH	1943
	Alnus glutinosa	Betulaceae	Eurasia	R(C)	<1913		
	Myosotis scorpioides	Boraginaceae	Eurasia	R(C)	1886	LO	1903

Taxon	Species	Family	Origin	Vector*	Great Lakes		St. Lawrence R
					Date	Site**	Date
	Rorippa nasturtium var. aquaticum	Brassicaceae	Eurasia	R(C)	1847	LO	1970
	Rorippa sylvestris	Bassicaceae	Eurasia	S(SB),R(C)	1884	LO	1934
	Butomus umbellatus	Butomaceae	Eurasia	S(SB)	1930	LM	1905
	Cabomba caroliniana	Cabombaceae	Southern US	R(AQ),R(A)	1935	LM	
	Stellaria aquatica	Caryophylliaceae	Eurasia	Unknown	1894	LSC	1965
	Chenopodium glaucum	Chenopodiaceae	Eurasia	RH	1867	LO	1904
	Carex acutiformis	Cyperaceae	Eurasia	Unknown	1951	LM	
	Carex disticha	Cyperaceae	Eurasia	NBS	1866	LO	1927
	Carex flacca	Cyperaceae	Eurasia	Unknown	1896	LE	1975
	Myriophyllum spicatum	Haloragaceae	Eurasia	R(AQ),S(F)	1949	LE	1945
	Hydrocharis morsus-ranae	Hydrocharitaceae	Rideau Canal	R(AQ),R(D)	1972	LO	1932
	Iris pseudacorus	Iridaceae	Eurasia	R(C)	1886	LO	1943
	Juncus compressus	Juncaceae	Eurasia	R(A)	1895	LE	1904
	Juncus gerardii	Juncaceae	Atlantic	S(SB)	1862	LM	IND
	Juncus inflexus	Juncaceae	Eurasia	Unknown	1922	LO	
	Lycopus asper	Labieae	Mississippi	R(A)	1892	LE	1942
	Lycopus europaeus	Labieae	Eurasia	S(SB)	1903	LO	1964
	Mentha gentilis	Labieae	Eurasia	R(C)	1915	LO	1890
	Mentha piperita	Lamiaceae	Eurasia	R(C)	1933	LH	1935
	Mentha spicata	Lamiaceae	Eurasia	R(C)	<1843	WID	1821
	Lythrum salicaria	Lythraceae	Eurasia	S(SB),C	1869	LO	1865
	Marsilea quadrifolia	Marcileaceae	Eurasia	R(C)	1925	LE	
	Nymphoides peltata	Menyanthaceae	Eurasia	R(A)	1930	LE	1950
	Najas marina	Najadaceae	Eurasia	S(BW)	1864	LO	1901
	Najas minor	Najadaceae	Eurasia	R(D)	1934	LE	
	Potamogeton crispus	Najadaceae	Eurasia	R(D),S(F)	1879	LO	1932
	Epilobium hirsutum	Onagraceae	Eurasia	R(A),S(SB)	1874	LO	1940
	Epilobium parviflorum	Onagraceae	Eurasia	Unknown	1966	LM	
	Agrostis gigantea	Poaceae	Eurasia	R(C)	1884	LS	1981
	Alopecurus geniculatus	Poaceae	Eurasia	R(C)	1882	LE	1899
	Echinochloa crus-galli	Poaceae	Eurasia	R(C),S(SB)	<1843	WID	1862
	Glyceria maxima	Poaceae	Eurasia	R(C),S(SB)	1940	LO	
	Poa trivialis	Poaceae	Eurasia	R(C),S(SB)	<1843	WID	1899
	Puccinellia distans	Poaceae	Eurasia	S(SB),RH	1893	LO	1984
	Polygonum caespitosum var. longisetum	Polygonaceae	Asia	Unknown	1960	LE	
	Polygonum persicaria	Polygonaceae	Unknown	Unknown	<1843	WID	1945
	Rumex longifolius	Polygonaceae	Eurasia	R(C)	1901	LS	1960
	Rumex obtusifolius	Polygonaceae	Eurasia	Unknown	<1840	WID	1821
	Lysimachia nummularia	Primulaceae	Eurasia	R(C)	1882	LO	1895
	Lysimachia vulgaris	Primulaceae	Eurasia	R(C)	1913	LO	
	Rhamnus frangula	Rhamnaceae	Eurasia	R(C)	<1913	LO	1970

Taxon	Species	Family	Origin	Vector*	Great Lakes		St. Lawrence R
					Date	Site**	Date
	Salix alba	Salicaceae	Eurasia	R(C)	<1886	WID	1945
	Salix fragilis	Salicaceae	Eurasia	R(C)	<1886	WID	1945
	Salix purpurea	Salicaceae	Eurasia	R(C)	<1886	WID	1943
	Veronica beccabunga	Scrophulariaceae	Eurasia	S(SB),R(C)	1915	LO	1905
	Solanum dulcamara	Solonaceae	Eurasia	R(C)	<1843	WID	1891
	Sparganium glomeratum	Sparganiaceae	Eurasia	Unknown	1941	LS	1931
	Trapa natans ■	Trapaceae	Eurasia	R(A),R(AQ)	<1959	LO	1998
	Typha angustifolia	Typhaceae	Eurasia	C,R(A)	1880s	LO	<1935
Invertebrate	*Argulus japonicus*	Argulidae	Asia	R(F), R(AQ)	<1988	LM	
	Bithynia tentaculata	Bithyniidae	Eurasia	S(SB),R(D)	1871	LM	1914
	Eubosmina coregoni	Bosminidae	Eurasia	S(BW)	1966	LM	1994
	+ *Eriocheir sinensis*	Branchiura	Asia	S(BW)	1965	LO	
	Orconectes limosus	Cambaridae	North America	Unknown			<1970
	+ *Orconectes rusticus*	Cambaridae	Mississipi	Unknown	1960	LS	
	Bythotrephes cederstroemi	Cercopagidae	Eurasia	S(BW)	1984	LH	
	+ *Cercopagis pengoi*	Cercopagidae	Eurasia	S(BW)	1998	LO	
	Cordylophora caspia	Clavidae	Unknown	R(A)	1956	LE	
	Corbicula fluminea	Corbiculidae	Asia	R(A),R(AQ)	1980	LE	
	+ *Corophium mucronatum*	Corophiidae	Ponto-Caspian	Unknown	1997	LSC	
	Tanysphyrus lemnae	Curcolionidae	Eurasia	Unknown	<1943	?	
	+ *Daphnia lumholtzi*	Daphniidae	Australia	Unknown	1999	LE	
	Skistodiaptomus pallidus	Diaptomidae	Mississippi	R(A),R(F)	1967	LO	
	Dreissena bugensis	Dreissenidae	Eurasia	S(BW)	1989	LO	1992
	Dreissena polymorpha	Dreissenidae	Eurasia	S(BW)	1986	LSC	1989
	+ *Echinogammarus ischnus*	Gammaridae	Eurasia	S(BW)	1995	LE	1997
	Gammarus fasciatus	Gammaridae	Atlantic	S(SB),S(BW)	<1940	?	IND
	Gillia altilis	Hydrobiidae	Atlantic	C	1918	LO	
	+ *Potamopyrgus antipodarum*	Hydrobiidae	New Zealand	Unknown	1991	LO	
	+ *Lophopodella carteri*	Lophopodidae	Asia	S(F)	1934	LE	1989
	Radix auricularia	Lymnaeidae	Eurasia	R(AQ), R(A)	1901	LM	1996 ?
	Ripistes parasita	Naididae	Eurasia	S(BW)	1980	LH	1983
	Eurytemora affinis	O: Calanoida	Widespread	S(BW)	1958	LO	1992
	Craspedacusta sowerbyi	Petasidae	Asia	R(A)	1933	LE	
	Dugesia polychroa	Planariidae	Eurasia	S(BW)	1968	LO	1968
	+ *Ichthyocotylurus pileatus*	Plathelmintha	Europe	R(F)	1994	LSC	
	Elimia virginica	Pleuroceridae	Atlantic	C	1860	LE	
	Glugea hertwigi	Protozoa	Eurasia	R(F)	1960	LE	1980
	Myxobolus cerebralis	Protozoa	Europe	R(F)	1968	LE	
	+ *Sphaeromyxa sevastopoli*	Protozoa	Black Sea	R(F)	1994	LSC	
	Aeromonas salmonicida	Pseudomonadacea	Unknown	R(F)	<1902	WID	Unknown
	Acentropus niveus	Pyralidae	Eurasia	R(A)	1950	LE/LO	
	Pisidium amnicum	Sphaeriidae	Eurasia	S(SB)	1897	LO	1978
	+ *Pisidium henslowanum*	Spaeriidae	Europe	Unknown	1905	WID	<1980

Taxon	Species	Family	Origin	Vector*	Great Lakes		St. Lawrence R
					Date	Site**	Date
	+ *Pisidium moitessierianum*	Spaeriidae	Europe	S(SB)	<1894	LE	
	+ *Pisidium supinum*	Spaeriidae	Europe	Unknown	1959	LO	
	Sphaerium corneum	Sphaeriidae	Eurasia	Unknown	1924	LO	1977
	Branchiura sowerbyi	Tubificidae	Asia	R(A)	1951	LM	
	Phallodrilus aquaedulcis	Tubificidae	Eurasia	S(BW)	1983	LO	
	Lasmigona subveridis	Unionidae	Atlantic	C	<1959	LE	
	Valvata piscinalis	Valvatidae	Eurasia	S(SB)	1897	LO	1991
	Cipangopaludina chinensis var. malleatus	Viviparidae	Asia	R(AQ)	1931	LO	<1980
	Cipangopaludina japonica	Viviparidae	Asia	R(D)	1940s	LE	
	Viviparus georgianus	Viviparidae	Mississippi	R(AQ)	<1906	LM	<1977
Fishes	*Enneacanthus gloriosus*	Centrarchidae	Eastern coast U.S.	R(AQ),R(F)	1971	LO	
	Lepomis humilis	Centrarchidae	Mississippi	R(A),R(AQ)	1929	LE	
	Lepomis microlophus	Centrarchidae	Mississippi	R(D), R(AC)	1928	LM	
	Alosa pseudoharengus	Clupeidae	Atlantic N. coast	C	1873	LO	IND
	+ *Alosa aestivalis*	Clupeidae	Atlantic N. coast	C	1995	LO	
	+ *Dorosoma cepedianum*	Clupeidae	Mississippi	C	1848	LE	1944
	Misgurnus anguillicaudatus	Cobitidae	Easthern Asia	R(A)	1939	LH	
	Carassius auratus	Cyprinidae	Asia	R(D),R(AQ)	<1878	WID	Unknown
	+ *Ctenopharyngodon idella*	Cyprinidae	Asia	R(D)	1986	LE	
	Cyprinus carpio	Cyprinidae	Eurasia	R(C),R(D)	1879	LE	1908
	+ *Hypophthalmichthys nobilis*	Cyprinidae	Asia	R(C)	1995	LE	
	Notropis buchanani	Cyprinidae	Mississippi	R(F)	1979	LSC	
	Phenacobius mirabilis	Cyprinidae	Mississippi	R(F)	1950	LE	
	Scardinius erythrophthalmus	Cyprinidae	Caspian-Aral Seas	R(F)	1955s	LE	1990
	Tinca tinca	Cyprinidae	Europe	R(A)			1991
	Apeltes quadracus	Gasterosteidae	Atlantic N. coast	S(BW)	1986	LS	IND
	+ *Gasterosteus aculeatus*	Gasterosteidae	Atlantic N. coast	C	1980	LH	IND
	Neogobius melanostomus	Gobiidae	Eurasia	S(BW)	1990	LSC	1997
	Proterorhinus marmoratus	Gobiidae	Eurasia	S(BW)	1990	LSC	
	Noturus insignis	Ictaluridae	Atlantic N. coast	C,R(F)	1928	LO	1971
	Osmerus mordax	Osmeridae	Atlantic N. coast	C,R(F)	1912	LM	IND
	Morone americana	Perchichthyidae	Atlantic N. coast	C	1950	LO	IND
	Gymnocephalus cernuus	Percidae	Eurasia	S(BW)	1986	LS	
	Petromyzon marinus	Petromyzontidae	Atlantic N. coast	C,S(F)	1835	LO	IND
	+ *Platichthys flesus*	Pleuronectidae	Europe	Unknown	1974	LE	
	Gambusia affinis	Poeciliidaae	Mississippi	R(D)	1923	LM	
	Oncorhynchus gorbuscha	Salmonidae	Pacific N. coast	R(A),R(F)	1956	LS	
	Oncorhynchus kisutch	Salmonidae	Pacific N. coast	R(D)	1933	LE	1972
	Oncorhynchus mykiss	Salmonidae	Pacific N. coast	R(D)	1876	LH	1950
	Oncorhynchus nerka	Salmonidae	Pacific N. coast	R(D)	1950	LO	
	Oncorhynchus tshawystcha	Salmonidae	Pacific N. coast	R(D)	1967	LM/LS	1983
	+ *Oncorrhynchus clarki*	Salmonidae	Pacific N. coast	R(A)			1941

Taxon	Species	Family	Origin	Vector*	Great Lakes		St. Lawrence R
					Date	Site**	Date
	Salmo trutta	Salmonidae	Eurasia	R(D)	1883	LO/LM	1890

* R(D): Deliberate; R(AQ): Release of aquarium; R(C): Release of cultivation; R(F): Release of organisms with bait or other fish; R(A): Release accidental; S(BW): Shipping with ballast water; S(SB): Shipping with solid ballast; S(F): Shipping with fouling; C: Canals.

**LO: Lake Ontario; LE: Lake Erie; LSC: Lake St. Clair; LH: Lake Huron; LM: Lake Michigan; LS: Lake Superior ; WID : Widespread.

🖬 : Species introduced in the Richelieu River.

Table 2. Origin of alien species introduced into the Great Lakes drainage basin and the St. Lawrence River

Origin	Great Lakes and St. Lawrence River *n* (%)		St. Lawrence River *n* (%)	
Eurasia	76	(47)	56	(66)
Europe	11	(7)	4	(5)
Asia	15	(9)	4	(5)
North America				
West coast	5	(3)	4	(5)
East coast	23*	(14)	5	(6)
Mississippi basin	11	(7)	3	(4)
Other point of origin or unknown	20	(12)	9	(11)

*Includes the 9 species that are endemic to the St. Lawrence River.

Table 3. Estimated times for alien species to transfer between the Great Lakes and the St. Lawrence River

Taxonomic group	No. of species	Transfer time[a] Mean ± SD	Median	Minimum	Maximum
Algae	8	31.5±19.1	21	17	69
Vascular plants	31	52.0±28.4	56	2	123
Invertebrates	17	41.7±33.5	43	1	95
Fishes	10	38.4±30.0	35	7	96
Vascular plants[b]	12	–25.2±34.5	–15	–3	–129

[a]Difference in date of first report (reports from Great Lakes precede those from the St. Lawrence River, except as noted otherwise) .
[b]Upstream transfer.
Note: SD = standard deviation.

Table 4. Numbers of alien species reported per decade since 1900 traced to shipping-related vectors, canals, other vectors and unknown sources

Decade	Shipping	Canals	Other vectors	Unknown	Total
1901–1910	2		5		7
1911–1920		1	8		9
1921–1930	1		7	2	10
1931–1940	5		9		14
1941–1950	1	1	5	4	11
1951–1960	2	1	6	3	12
1961–1970	10		4	1	15
1971–1980	11	1	4	2	18
1981–1990	9		2		11
1991–2000	5	1	1	2	9