Exotic Species and the Integrity of the Great Lakes

Lessons from the past

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One of the most pervasive and damaging anthropogenic impacts on the world's ecosystems is the introduction of nonindigenous species (Elton 1958, Mooney and Drake 1989). In the United States, at least 4500 nonindigenous species including several thousand plant and insect species and several hundred non-native vertebrate, mollusk, fish, and plant pathogen species have established free-living populations (OTA 1993). Approximately 15% of these nonindigenous species have caused severe harm affecting agriculture, industry, human health, and the natural environment (OTA 1993).

Since the early 1800s, some of the greatest ecological disasters in North America's Great Lakes, the world's largest freshwater resource, have resulted from biological invasions. The cumulative effects of many nonindigenous species on the natural structure of the Great Lakes ecosystem have compromised its biological integrity. In addition to this loss, some individual invaders such as the sea lamprey *(Petromyzon marinus)* and the zebra mussel *(Dreissena polymorpha)* have caused substantial economic hardships and ecological instability. Human activities such as the construction of the Erie Canal and the St. Lawrence Seaway have played a major role in the introduction of nonindigenous species to the Great Lakes ecosystem. At present, species introductions continue to pose a threat to the integrity of the lakes.

Cumulative effects of many nonindigenous species have compromised the Great Lakes ecosystem

In this article, we review new documentation of the extent, timing, origins, dispersal mechanisms, and impacts of biological invasions in the Great Lakes basin. Eight states and one province claim Great Lakes shoreline, and major port cities such as Chicago and Toronto use the Great Lakes as part of a national and international trade route—the St. Lawrence Seaway (Figure 1). The Great Lakes play a major role in the economies of these regions, and the string of ecological disasters associated with biological invasions must be stopped. We hope that lessons from the past help to prevent future invasions.

Great Lakes exotic species

The Great Lakes currently host at least 139 nonindigenous fishes, invertebrates, fish disease pathogens, plants, and algae (Table 1; Mills et al. 1993a). These species are successfully reproducing, were not present in the Great Lakes before 1800, and were transported into the ecosystem by humans. The majority are aquatic plants (including submerged plants, marsh plants, and shoreline trees and shrubs), fish, algae, mollusks and crustaceans.

Mills et al. (1993a) discuss Great Lakes exotic species and detail their introductions at length. Aquatic plants and fish, the largest groups of nonindigenous species, have historically been among the best studied groups of freshwater organisms. Groups that require microscopic analysis, such as protozoans, nematodes, rotifers, gastrotriches, bryozoans, and sponges, are likely to contain exotics that remain undiscovered or have been mistakenly considered as Great Lakes natives. Taxonomists had not studied these groups in the Great Lakes until entry mechanisms were in place for decades or even hundreds of years.

Most recently, studies in popula-

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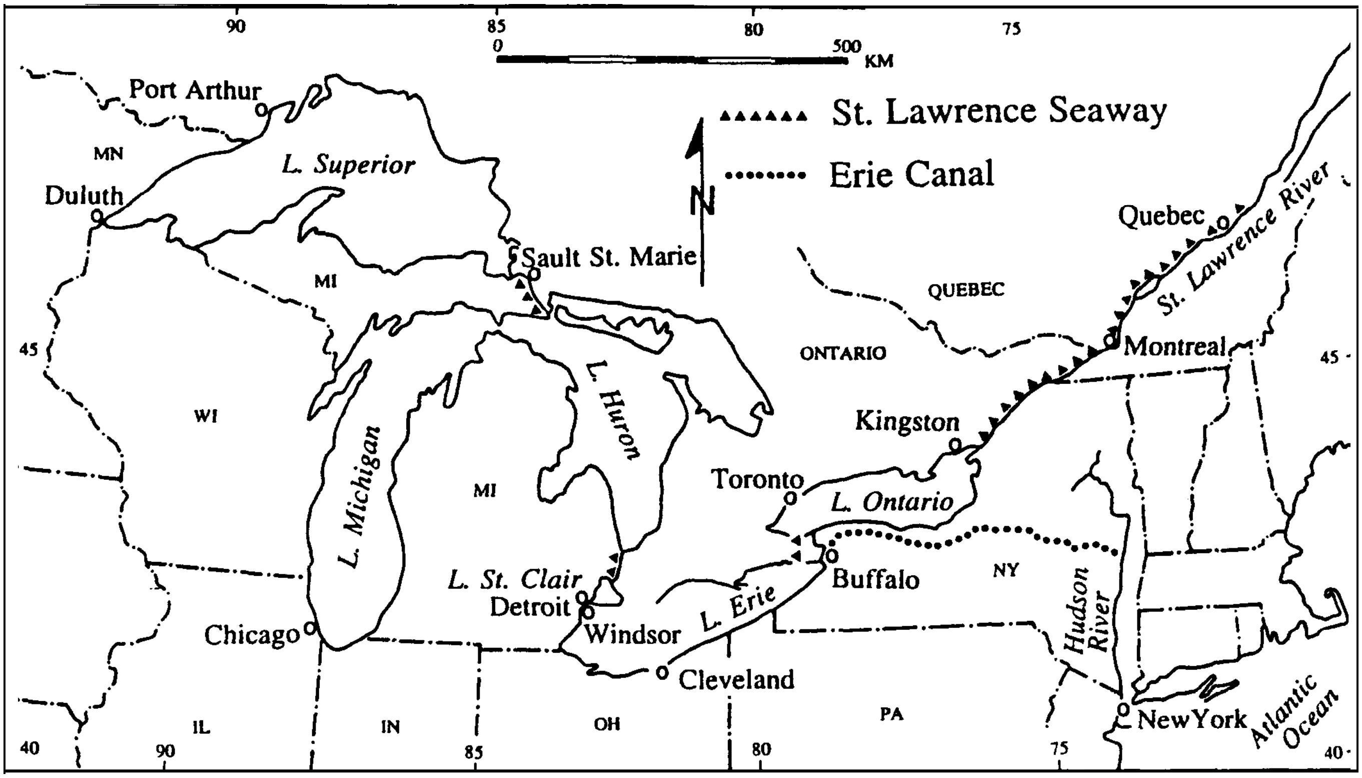


Figure 1. A map of the Laurentian Great Lakes including the St. Lawrence Seaway and the Erie Canal.

tion genetics have been shown to be useful in identifying introduced species that are morphologically similar to a native species or may have been introduced before biological surveys. For example, an allozyme survey by Taylor and Hebert (1993) discovered patterns of genetic variation in Great Lakes populations of Daphnia galeata that indicate the previously undiscovered introduction of a European form of the species during the late 1970s or early 1980s.

Great Lakes exotic species are native to eight different geographic regions of the world, which include Europe and Asia (Eurasia), the Atlantic and Pacific Coasts of North America, southern United States, Midwestern United States, and the Mississippi River drainage system. Most exotic species in the Great Lakes, however, are native to Eurasia (55%) and the Atlantic Coast (13%). The large number of introductions from Eurasia is most likely associated with the settlement of the basin by Europeans who transported goods primarily from Europe (Hatcher 1944) and to the similarity of the climates of the Great Lakes region and Europe. Some of these species did not invade directly from Eurasia. For example, the Asiatic clam *Corbicula fluminea,* was introduced to the west coast of North America and then expanded its range to other parts of the United States, including the Great Lakes.

Invasion history

Identifying introduced species and their native geographic ranges does not address the role of human activity in this environmental problem. The history of exploration, colonization, settlement, and commercial development of the Great Lakes by European settlers spans almost four centuries. Throughout this period, nonindigenous aquatic animal and plant species have been introduced both intentionally and accidentally. A variety of entry mechanisms have acted singly or jointly in these invasions, which have intensified since the Europeans' discovery of the Great Lakes.

1800–1870. In 1825 a prophetic ceremony took place as the first barge plying the Erie Canal from Lake Erie to the Atlantic Ocean arrived in New York Harbor. This barge brought a keg of Lake Erie water for New York's Governor DeWitt Clinton to dump into the Harbor "in grave symbolic rites" (Hatcher and Walter 1963). Vials of water from the Thames, Seine, Elbe, Rhine, Orinoco, Ganges, and Nile Rivers were also emptied during the ceremony. Boats returning to Lake Erie took water from the Atlantic Ocean to complete the cycle (Hatcher 1944). This exchange of waters foreshadowed the large-scale ballast water releases that now introduce organisms from around the world into the Great Lakes.

The Erie Canal is part of a complex network of canals. They dissolved barriers that had previously kept ships from passing from one watershed to another and organisms from dispersing into the Great Lakes from other drainage basins. For example, a snail, *Elimia virginica,* is thought to have migrated into the Great Lakes drainage from the Hudson River drainage basin through the Erie Canal in the mid-1800s. The first St. Lawrence River canal system, completed in the mid-1800s (Figure 1), represents the start of shipping between Great Lakes and distant North American

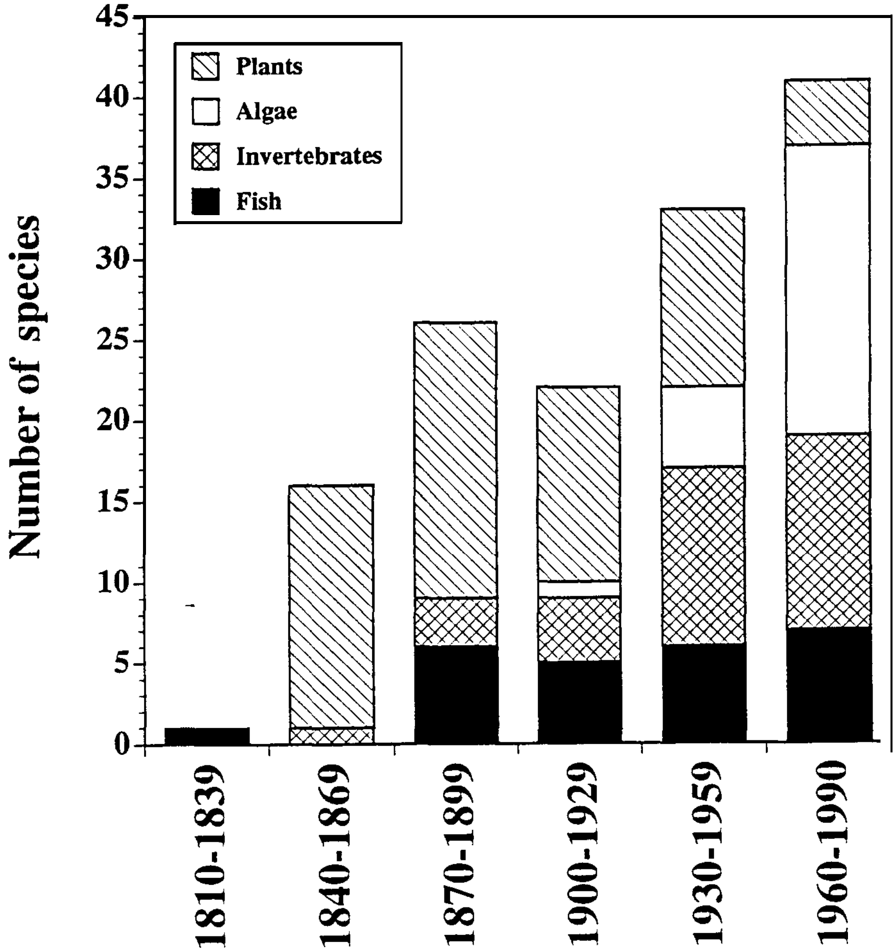


Figure 2. A timeline of Great Lakes introductions (N=139) sorted by taxonomic group. (From Mills et al. 1993a.)

and European ports (Larson 1983, Mills 1910). These canals not only provided a conduit for migration of organisms into the Great Lakes, but they also allowed Great Lakes' species to spread into adjoining waterways.

Historically, ships plying the Erie and St. Lawrence canal systems used solid ballast, including rocks, mud, sand, or shoreline debris, for stabilization. The use of solid ballast enabled many plants and invertebrates to be transported large distances to North America (Brown 1879). As a ship reached port to take on cargo, the ballast was generally thrown overboard or disposed of in designated dumping grounds. Animal bedding and packaging materials were generally discarded along with solid ballast, making plant introductions with these materials difficult to distinguish from ballast introductions. The hay and straw used as fodder and bedding for the towpath mules could have contained non-native plants that were loaded in New York and deposited in Buffalo. During this period, purple loosestrife *(Lythrum salicaria),* black-grass rush (Juncus *gerardii),* a sedge *(Carex disticha),* and spiny naiad *(Nujas marina)* were probably introduced in this manner.

On the hulls of some of these boats entering the Great Lakes were fouling organisms, organisms that attach to solid objects. For example, the sea lamprey is thought to have gained access to the Great Lakes in part either by attaching to the hulls of ships entering from other waterways or by migrating through newly constructed canals (Morman et al. 1980). Because solid ballast and fouling organisms were being brought into the Great Lakes long before many biological surveys were done, some species previously thought to be native may in fact have been introduced.

The release of plants from cultivation has been occurring since colonial times when settlers imported non-native plants to use for medicinal purposes, for example, bittersweet nightshade *(Solarium dulcamara;* Torrey 1843); gastronomical purposes, for example, watercress *(Rorippa nasturtium aquaticum;* Green 1962); and later, ornamental purposes, for example, yellow flag *(Iris pseudacorus;* Judd 1953). When the plants were cultivated, they were normally not intended to spread. But by the time the earliest comprehensive floras of parts of the Great Lakes region were published (Torrey 1843), many nonindigenous cultivated plants were established and widespread. For example, poison hemlock *(Conium maculatum),* bittersweet nightshade, peppermint *(Mentha piperita),* and spearmint *(Mentha spicata)* were established before the publication of the earliest New York flora in 1843 (Torrey 1843). In 1847, watercress was discovered in Niagara Falls.

By 1860, railroads connected the Atlantic Coast to the Great Lakes (Hatcher 1944). The construction of railroads and roads provided newly disturbed habitat and promoted dispersal of plants into new areas. Along areas of disturbed soil associated with the construction of railroad tracks. the migration of plants occurred from both the Atlantic Coast and the Midwest into the Great Lakes basin. In the 1860s, oak-leafed goosefoot *(Chenopodium glaucum)* was discovered in the Great Lakes and probably gained access to and spread within the Great Lakes with the aid of soil disturbance associated with the building of railroad beds.

Seventeen introduced species, predominately plants, had established populations in the Great Lakes drainage basin by 1870 (Figure 2). Fish, plants, and mollusks were the only taxonomic groups surveyed within this period, and each of these taxa contain species introduced before 1870. No doubt other species were cryptically introduced and established during this period, which was prior to the description of the flora and fauna by early Great Lakes taxonomists.

1870-1930. In the 1880s, new technologically advanced ships began using ballast water for stabilization. Because the switch from solid to water ballast did not occur immediately, introductions by both vectors were possible during the late 1800s and early 1900s. Improvements on canals enabled larger ships to enter the Great Lakes, and thus increased the potential for new invaders through ships' ballast. Between 1870 and 1930, five species of plants and three invertebrates were introduced in solid ballast. One species of diatom, *Stephanodiscus binderanus,* has been identified as introduced in ballast water. In 1893, weeping alkali grass *(Puccinellia distans),* a coastal salt-marsh species, was discovered in the Great Lakes basin; it had probably gained access through several vectors including solid ballast and railroad migration.

Government agencies have deliberately introduced fish species, mostly to enhance fisheries, into the Great Lakes since the 1870s (Emery 1985). Species introduced include commercially valuable fishes like brown trout *(Salmo trutta),* chinook salmon *(Oncorhynchus tshawy - tscha),* and rainbow trout *(Oncorhynchus mykiss),* as well as nuisance species like the common carp (Cyprinus *carpio).* Although much attention is given to the introduction of game fish like salmon or trout, species like the western mosquitofish *(Gambusia affinis)* for mosquito control—and the redear sunfish *(Lepomis microlophus)*—a panfish—were also deliberately introduced in the 1920s. Deliberate mollusk introductions may also have occurred by the mid-1800s (Kew 1893) but remain undocumented. By the 1930s, scientists recognized that deliberately introduced plants had become established. Along with deliberately released exotic species was the potential for the unintentional release of associated organisms, such as disease pathogens, other fish species, and plankton present in the transport water.

From 1870 to 1930, the release of plants from cultivation was a common entry mechanism. Five species of trees and shrubs—black alder *(Alnus glutinosa),* white willow *(Salix alba),* crack willow (Salix *fragilis),* purple willow *(Salix purpurea),* and glossy buckthorn *(Rhamnus frangala)*— were imported for use as ornamental, medicines, or supplies for basket weaving. These trees now line many banks and shores of the Great Lakes. Of the seven other plants introduced during this period, six are garden plants. The seventh, redtop *(Agrostis gigantea),* is cultivated as a forage crop for livestock and has invaded marshes and stream or river banks in the Great Lakes.

The aquarium trade can also serve as a source for introduced species. When aquarium owners become tired of their pets, they often discard them into the nearest body of water. The banded mystery snail *(Viviparus georgianus),* a native of the Mississippi River drainage basin, was introduced into the Great Lakes before 1910 as a result of aquarium dumping. Numerous magazines such as *The Aquarium* and *Aquariana,* which were published in the early 1900s, documented the extent of the aquarium trade and described animal and plant species now found in the Great Lakes.

Forty-eight species have been documented as being introduced between 1870 and 1930 (Figure 2). The majority were plants, but a substantial number of fish and invertebrate species have been discovered to be introduced during this time. Most (63%) of the exotics established during this period were associated with unintentional release.

Table 1. Relative abundance of taxonomic groups of introduced species in the Great Lakes.

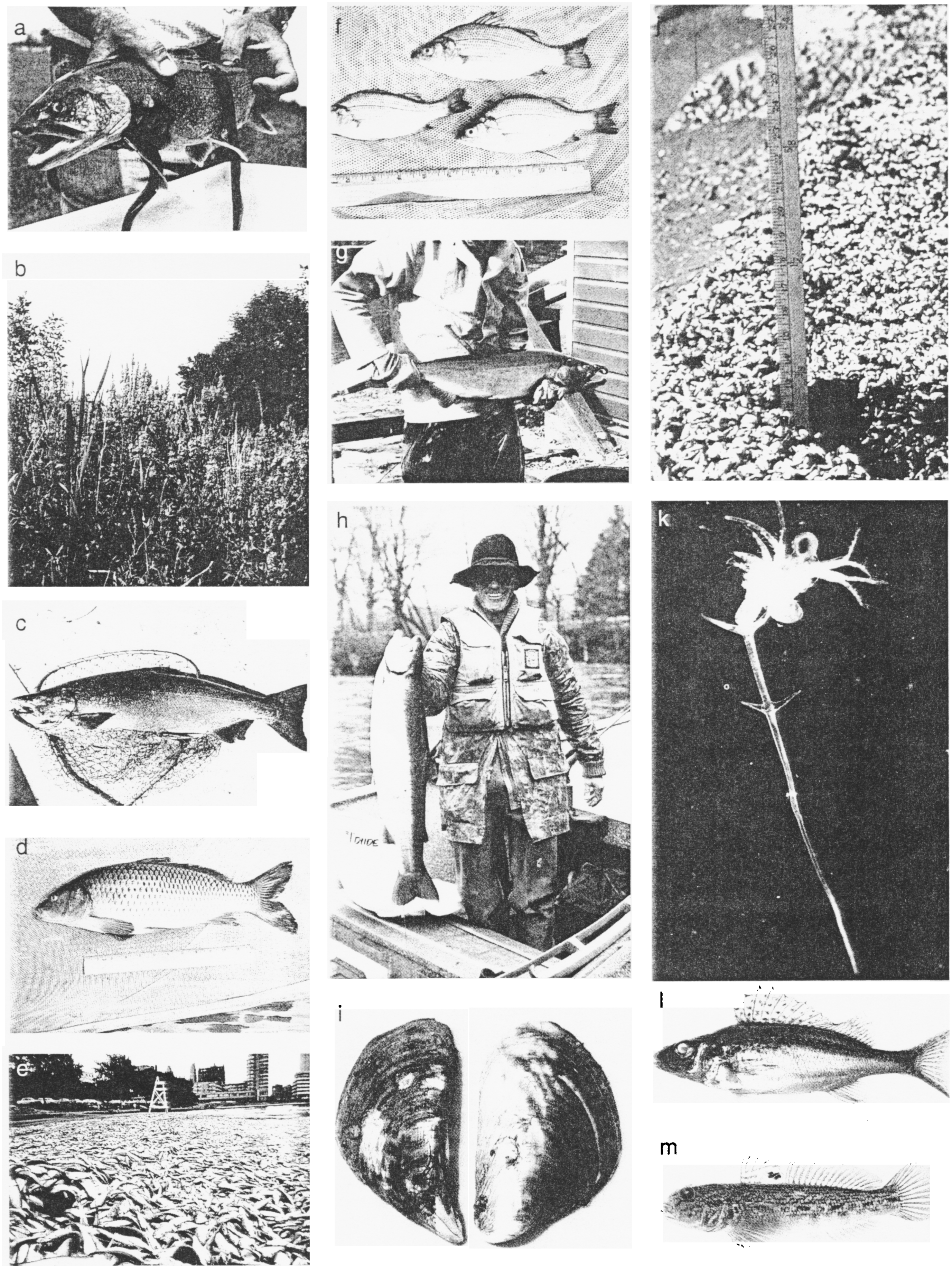
Taxonomic group	Percentage of introduced species
Fish	18
Invertebrates	
Mollusks	10
Crustaceans	4
Oligochaetes	2
Other invertebrates"	5
Fish disease pathogens	2
Algae	17
Plants	
Submerged plants	7
Marsh plants	31
Shoreline trees and shrubs	4

*Other invertebrates include protozoans, nematodes, rotifers, gastriches, bryozoans, and sponges.

1930–1990. As more ships began using ballast water for stabilization and as waterways connecting the Great Lakes to the ocean were expanded, ballast-water introductions became more prevalent. When the St. Lawrence Seaway opened in 1959 (Ashworth 1986), transoceanic trade between Great Lakes ports, such as Chicago, Toronto, and Duluth, and ports from around the world intensified (Figure 1). After the shallow canals in the St. Lawrence were expanded, the amount of ballast water released from large ships into the lakes increased dramatically, and there was greatly increased risk that new invaders would become established in the system. During the 1970s, many diatom species that were probably introduced in ballast water were discovered in the Great Lakes. And during the 1980s, the number of ballast-water releases of fish and invertebrates increased. h-t the early to mid-1980s, seaway ship traffic was higher than more recentlly.[1] During this period, zebra and quagga mussels, spiny water flea, tubenose and round gobies, and Eurasian ruffe became established.

During the 1960s and 1970s, the exotic fish trade was a multimillion-dollar business in the United States (Conroy 1975). Many of the tropical freshwater and saltwater fish that have been introduced to southern North America (Courtenay et al. 1984) are not likely to become established in the Great Lakes because winter temperatures drop below their tolerance limits. Aquarium *releases,* however, do occur within

[1]Captain Jim Perkins, 1992, personal communication, St. Lawrence Seaway Authority.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the Great Lakes. For example, the oriental weatherfish *(Misgurnus anguillicaudatus)* was introduced into Lake Michigan in 1939 by an aquaculture facility that was breeding it for sale as an aquarium fish.

Deliberate stocking of fish continued to augment existing introduced salmon and trout fisheries through the twentieth century. Two additional species of salmon, coho salmon *(Oncorhynchus kisutch)* and kokanee *(Oncorhynchus nerka),* were introduced in 1933 and 1950. In 1956, pink salmon *(Oncorhynchus gorbuscha),* which were to be released in Hudson Bay tributaries, were accidentally introduced into Lake Superior from a fish hatchery. These fish survived to reproduce and have spread into all the Great Lakes.

Recently, the bait fish industry began to culture rudd *(Scardinius erythrophthalmus)* and sell them within and adjacent to the Great Lakes basin. These bait fish, released by fishermen, had become established by 1989 in the Great Lakes basin. Another fish, the ghost shiner *(Notropis buchanani)* was discovered in the Great Lakes in Ontario in 1979 in a location 510 km from the nearest known ghost shiner population. This transfer was probably made in a fisherman's bait bucket.

Between 1930 and 1990, 74 species were introduced, of which more than one-half became established subsequent to the opening of the St. Lawrence Seaway in 1959 (Figure 2). Since 1930, the escape of plants from cultivation in the Great Lakes basin has declined, the number of fish has increased slightly, and the number of invertebrates and algal species has increased.

Opposite page: A gallery of Great Lakes exotics. Sea lamprey (a) seen attached to lake trout and the purple loosestrife (b) are among the earliest invaders of the Great Lakes. Stocking of chinook salmon (c) and common carp (d) began in the 1870s. Buildup of alewife in southern Lake Michigan (e) led to massive dieoffs near Chicago in the 1960s. White perch (f) became established in the 1950s, and both coho (g) and steelhead salmon (h) were intentionally introduced to establish a sport fishery. The arrival of zebra mussel (i, left) and quagga mussel (i, right) in the mid-1980s set the stage for long-term ecological and economic impacts. Shells of these mussels one foot deep (i) have accumulated on beaches in Lake Erie after storms. Recent introductions include spiny water flea (k), Eurasian ruffe (l), and round gobie (m). Credits: (a) US Fish and Wildlife Service; (b, d, f, i) Cornell University Biological Field Station; (c, g, h) New York Department of Environmental Conservation; (e) Center for Limnology, University of Wisconsin; (j) Robert Sutherland, Ontario Ministry of Natural Resources; (k) D. R. Barnhisel, Michigan Technological University; (1) James Selgeby, National Biological Survey, Lake Superior Biological Station; and (m) David Jude, Center for Great Lakes and Aquatic Sciences, University of Michigan.

Post-invasion impacts of Great Lakes exotics

At least 139 exotic species have been introduced to the Great Lakes, yet we know little about the roles they play in the modern-day community structure or how the invaders have changed the communities invaded. Introductions may lead to extensive ecological changes through a variety of processes including interspecific competition, disturbance, and predation (Krueger and May 1991). Worldwide, the magnitude of the exotic species problem is enormous; the flora of most regions contain 10%-30% exotic species (Heywood 1989). Although the number of species, dispersal rates, and the factors controlling their movement and establishment has received much attention recently. (Groves and Burden 1986, Mooney and Drake 1989), the ecological effects of introduced species worldwide including the Great Lakes are still poorly known (Pimm 1991, Vitousek 1986). All established exotics use some resources (e.g., space or food) that may be usurped from native or previously introduced species. However, not all exotics are harmful nor do they always disturb ecosystems in social and economic terms.

Exotic species have contributed significantly to the biological artificiality of the Great Lakes ecosystem and have had impacts on virtually every ecological niche. For this large freshwater ecosystem, almost 10% of established exotic species have had serious impacts.

Of the fish, 50%. have been shown to have important ecological and / or economic consequences, and some of the earliest introductions have had long-term impacts. The sea lamprey, a parasitic fish, has had a catastrophic impact on native lake trout populations resulting in millions of dollars in damages and losses to commercial fisheries. In the late 1960s, the large buildup of alewife populations accelerated the collapse of coregonid (e.g., lake whitefish and bloater) populations, adversely affected yellow perch and other native species, and caused significant economic losses to lakeside communities in the watershed (Brandt et al. 1987, Smith 1970). Subsequently, the alewife became an important prey fish for introduced salmon (Emery 1985, Stewart et al. 1981). However, artificial propagation of salmonids in such Great Lakes as Michigan and Ontario has resulted in ecosystems that have recently come into fragile "balance" with their food supply (Koonce and Jones 1994). The white perch used the Hudson River and Erie Canal as a gateway to the Great Lakes (Christie 1973, Hurley 1986) where it has caused substantial population changes in the native fish species and community stability (Boileau 1985). At present, the potential for competition between white perch and native species remains high (Schaeffer and Margraf 1986).

The stocking of rainbow trout, salmon, and common carp began in the 1870s (Emery 1985, Scott and Crossman 1973). These species were intended to augment the declining commercial food fishes of the Atlantic Coast (e.g., American shad and Atlantic salmon) and the Great Lakes (e.g., lake whitefish and lake trout). Carp never became popular and by the 1890s were considered a problem because of their impacts on nearshore benthic habitats used by more favored fish species and waterfowl (lMcCrimmon 1968). The salmonids, whether introduced deliberately into the Great Lakes to enhance the sport fishery or unintentionally as in the case of the pink salmon, have had profound and permanent ecological / genetic effects on

Table 2. Exotic species considered to have substantial impacts on the present Great Lakes resources.

Organism	When established	Impact
Sea lamprey	1830s	Caused decline of native lake trout populations
Purple loosestrife	1869	Competes with native plants causing loss of habitat for waterfowl
Alewife	1873	Suppresses native fish species, became important prey fish for salmon
Chinook salmon	1873	Preys upon Great Lakes fishes, became a valuable sport fish
Common carp	1879	Destroys habitat of favored fish species and waterfowl
Brown trout	1883	Preys upon Great Lakes fishes, became a valuable sport fish
Furunculosis	1902	Infects Great Lakes fishes
Coho salmon	1933	Preys upon Great Lakes fishes, became a valuable sport fish
White perch	1950s	Competes with native fish species
Eurasian watermilfoil	1952	Competes with native plants, affected recreational use of water
Glugea hertwigi	*1960*	Parasitizes fish
Eurasian ruffe	1986	Competes with native fish species
Zebra mussel	1988	Biofouls hard substrate, competed with and altered habitat of native species

the fish fauna. Ecological effects of salmonid introductions include competition, predation on native salmonids and other fishes, and the introduction of parasites and disease on native fish (Krueger and May 1991). Direct genetic effects from stocked salmonids are caused by interbreeding with native species, while indirect effects may result through selective forces and/or a reduction of effective population size, genetic drift, and inbreeding.

The European ruffe, a spiny rayed percid introduced with ballast water, was first identified in Lake Superior in 1986 (Pratt et al. 1992). The ruffe has the potential to disperse throughout much of North America and become a major competitor with other fish species throughout the Great Lakes. Should ruffe become established in Lake Erie, the site of the world's largest yellow perch and walleye fisheries, the potential economic impact could reach an annual economic loss of $90 million (Anonymous 1992).

Introduced mollusks have also posed a threat to the Great Lakes. The faucet snail, *Bithynia tentaculata,* spread throughout the Great Lakes basin and, by the early 1900s, the snail infested municipal water supplies from intake pipes to household faucets (Baker 1902) and most likely outcompeted many native mollusks (Harman and Forney 1970). Although the plumbing problems were resolved, the snail remains abundant in the Great Lakes.

The zebra mussel, which arrived in 1986 (Hebert et al. 1989), and the quagga mussel *Dreissena bugensis* (Spidle et al. in press) are two major fouling organisms of water intake and nautical and littoral structures in the Great Lakes (Griffiths et al. 1989). These mollusks are expected to result in billions of dollars in control and impact costs. Recent invasion of these two dreissends in both nearshore and profundal sediments of Great Lakes waters represents a disturbance that is predicted to cause the loss of native unionids and is likely to have long-term impacts on the structure of pelagic and benthic communities (Dermott and Munawar 1993, Ludyanskiy et al. 1993, Mills et al. 1993).

Introduced plant species outnumber all other groups of introduced organisms, and the impacts of most on native flora and fauna is unknown. However, massive beds of a nonindigenous submerged aquatic plant, Eurasian watermilfoil *(Myriophyllum spicatum),* often impair recreational use, including swimming and boat travel, in the smaller and shallower lakes in the Great Lakes basin.

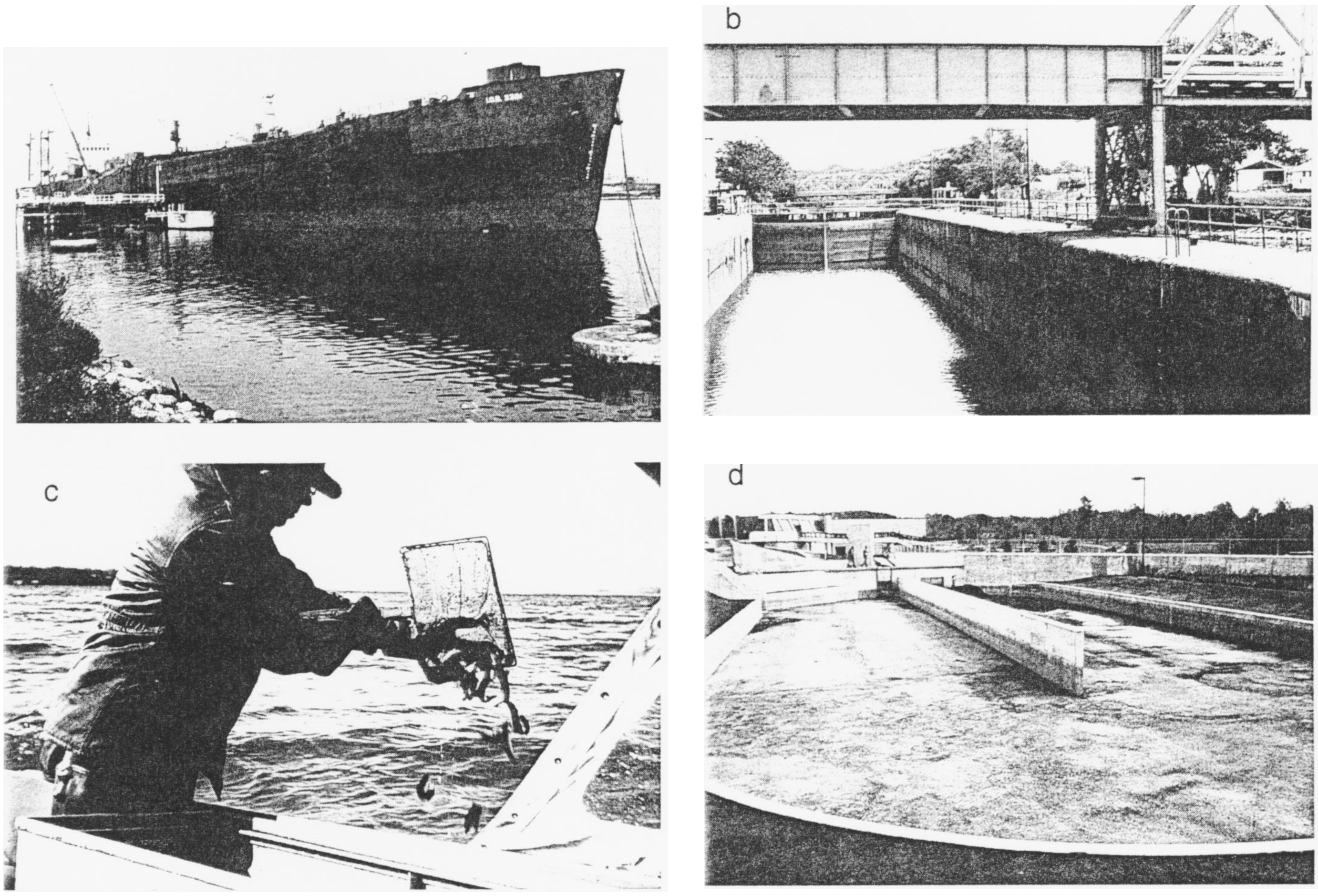
In addition, purple loosestrife inhabits marshland in large monospecific stands, outcompeting native cattails *(Typha* sp.) and other plants, making these areas less suitable as wildlife habitat and for farming (Malecki et al. 1993, Rawinski and Malecki 1984). Malecki et al. (1993) describe an ongoing program of biological control for purple loosestrife. Three species of insects—a weevil and two beetles—have been introduced to control populations of the invasive weed.

Surprisingly, few disease pathogens non-native to the Great Lakes have been identified. The salmon whirling disease and furunculosis are associated with fish and fish hatcheries and have had significant impacts. The routine introduction of new fish into hatchery facilities makes them vulnerable to outbreaks of disease (Bullock et al. 1983, Wolf and Markiw 1985).

Vulnerability of the Great Lakes to invasion

The long history of invasions and increasing rate of introductions—now averaging one organism per year—clearly indicate that the Great Lakes are highly vulnerable to invasion. Ecologists have traditionally believed that disturbance is the most important factor that influences the vulnerability of a system to invasion—disturbed communities are thought to be less resistant to invasions than undisturbed communities (Elton 1958). Another theory, however, holds that inoculation rates, the rate at which organisms are brought into the ecosystem, determine the vulnerability of an ecosystem to invasion (Groves and Burden 1986, Mooney and Drake 1989).

In the case of the Great Lakes since 1959, the level of human-generated disturbance may be linked to both the volume of inoculation water (e.g., the number of colonists) and the rate new organisms are inoculated into the Great Lakes, thus obscuring the distinction between these two theories. In addition, the vector of ballast water itself may have changed, due to improved water quality inside ballast tanks, larger vessels bringing greater amounts of water per ship, and faster ships, decreasing at-sea time and therefore possibly increasing in situ survival.



major tronsport vectors through which exotic organisms have entered the Great Lakes: (a) shipping, (b) canals, (c) deliberate release (here, stocking of fish), (d) unintentional release (here, escape from fish hatcheries], and (e) disturbance of soil through construction of railroads and highways. Credits: (a) Photo courtesy of James T. Carlton; (b-e) Photos courtesy of Cornell University Biological Field Station.

Nearly 30% of the exotic species of the Great Lakes have been discovered since 1959, a surge which has coincided with the opening of the St. Lawrence Seaway. The seaway allows large volumes of foreign water to enter the Great Lakes from the ballast water of ships, thereby increasing the inoculation rate and the risk that non-native organisms will become established.

Other factors have likely influenced the recent surge in unplanned introductions. These factors include the improved quality of donor habitats in some parts of the world and the improved quality of the Great Lakes as a receiver region (Scavia et al. 1986).

Human-mediated disturbance, however, is not recent in the Great Lakes basin. The first well-known alteration was regional deforestation for agriculture and growth of the lumber industry in the mid-1800s (Stoermer et al. 1985). Such a disturbance greatly altered the Great Lakes ecosystem and probably made it vulnerable to invasion, although detailed studies of many taxonomic groups from this period are lacking. Cultural eutrophication, contaminants, habitat degradation, and overexploitation of fish stocks are just a few additional anthropogenic factors that historically have likely had indirect influence on patterns of establishment of exotics in the Great Lakes.

Future invaders

Predicting potential invaders to the Great Lakes would clearly be useful in preventing future nonindigenous pests. Scientists have long considered the attributes of potential invaders contemplating both theoretical and applied aspects. Theoretical attributes of a typical invasive species and the extraordinary biological and ecological diversity of actual invaders have led to conclusions that the search for universal characteristics of invasive species is difficult at best.

At the general level, however, invasive species in donor regions usually have such characteristics as high abundance, short generation time, polyphagy, the ability to occupy a broad diversity of habitats, broad physiological plasticity, and often high genetic variability. The recent introduction of the zebra mussel was a predictable invasion to the Great Lakes. The species had a remarkable invasion history in Europe, could interface with an intercontinental transfer mechanism, and was adaptable to a wide range of habitats.

However. Carlton et al.[2] note that there appears to be no correlation between invader's range of distribution in a donor region and its potential to colonize a new recipient region. While many exotics in the Great Lakes (e.g., mollusks) have broad distribution patterns throughout Europe, others have comparable limited distributions (such as the gobies *Neogobius* and *Proterorhinus* and the spiny waterflea *Bythotrephes).*

Carlton, Secor, and Mills[3] predict that the Antipodean snail. *Potamopyrus antipodarum,* and the Caspian amphipod, *Corophium curvispinum,* will invade North America and the Great Lakes from Europe. Both of these organisms have an extensive invasion history in Europe, interface with transcontinental transport mechanisms, are highly fecund, and tolerate a wide range of environmental conditions. Interestingly, the Antipodean snail was discovered in Idaho in the 1980s. This new population of highly invasive species provides another source for a future Great Lakes introduced species.

Future invasions in the Great Lakes will occur, and some will have substantial negative consequences to the Great Lakes environment. Movements of organisms within the lakes. such as the arrival of the ruffe in the lower, warmer, more eutrophic Lakes Erie and Ontario, will predictable rival intercontinental inproductions in their impact. The timing and extent of invasions is likely to depend on a great many factors, including the species involved, the mode and tempo of transport mechanisms, and changing environmental conditions both in donor regions and the Great Lakes. Enhanced ability to recognize potential future invaders and knowledge of the enemy is critical toward preventing future unwanted introductions into the Great Lakes. Knowledge of such factors would enhance our ability to develop effective prevention 'and control strategies (Mills et al. 1993 b).

In May 1989—less than a year after zebra mussels were first found by scientists in the Great Lakes—the Canadian government had in place voluntary guidelines requesting ships to exchange their ballast water in the open ocean prior to entering the Great Lakes. In November 1990, the US Congress passed the Nonindigenous Aquatic Nuisance Species Act, known generally as the ballast water or the zebra mussel legislation. This law called for research and education on zebra mussels. addressed concerns about intentional introductions and the use of exotic species in research, and tackled the issue of ballast water.

Under the act, the United States adopted guidelines in May 1991 similar to those of Canada, and in May 1993 these guidelines became law—the first and onlv ballast-water law in the world. The law requires that ships that have operated outside the waters of the United States and Canada and that intend to enter the Great Lakes with ballast water must have exchanged that water on the high seas (in water depths of more than 2000 meters), and that the water must be no less than 30 parts per thousand (o/oo) salinity (full salinity open–Atlantic Ocean water is, for example, 35-36 o/oo, and thus the law recognizes some potential mixing and dilution with the previous ballast water). Supplementary legislation in 1992 amended the act, extending the requirement (effective this year) for exchanging ballast water to ships intending to enter the Hudson River, a potential backdoor to the Great Lakes for exotic species.

Open-ocean ballast exchange is likely to be particularly effective in the prevention of new freshwater species entering the Great Lakes—not only would much of the original water be released in the high seas, but the high salinity of ocean water further acts as a chemical biocide for any freshwater species that may remain in the ship after exchange has been undertaken. Brackish-water organisms that could become established in the Great Lakes (and estuarine and marine organisms being carried in ballast into coastal US ports in general), could, however, remain alive in exchanged ballast water, as they would not be killed by the higher ocean salinities. Such organisms typically remain in the ballast tanks when the exchange process is incomplete, as it often is—many vessels either would not (due to weather conditions) or could not (due to design) pump out every last gallon of their ballast water before pumping in new water (Locke et al. 1993).

In response to this concern, Congress called for a detailed exploration of alternative ballast-water control strategies, such that when ballast exchange was impossible or incomplete other options would be available. These studies, mandated under the act, are in progress, and focus on the application of water quality control technology (such as microfiltration, thermal treatment, ultraviolet, ozonation, and other chemical treatments).

Finally, future legislative and regulatory efforts must also consider the threat to the Great Lakes

[2]Carlton, J. T., C. L. Secor, and E. L. Mills, 1994, manuscript submitted.
'See footnote 2.

from importation, culture, and distribution of bait, as well as from organisms associated with the aquarium trade. As long as the Great Lakes are subject to human-mediated transfer, the world's largest freshwater resource will continue to be at risk from invasions.

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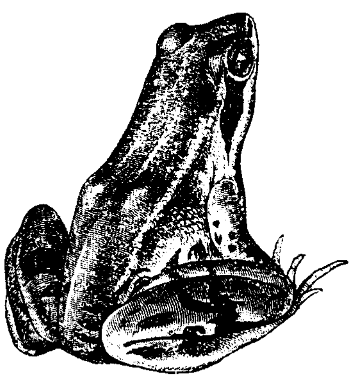

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