J. Great Lakes Res. 19(1):1-54
Internat. Assoc. Great Lakes Res., 1993

Exotic Species in the Great Lakes: A History of Biotic Crises and Anthropogenic Introductions

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ABSTRACT. *Through literature review, we documented introductions of non-indigenous aquatic flora and fauna into the Great Lakes basin since the early 1800s. We focused on the origin, probable mechanism(s) of introduction and the date and locality of first discovery of Great Lakes exotic species. The Laurentian Great Lakes have been subject to invasion by exotic species since settlement of the region by Europeans. Since the 1800s, 139 non-indigenous aquatic organisms have become established in the Great Lakes. The bulk of these organisms has been represented by plants (59), fishes (25), algae (24), and mollusks (14). Most species are native to Eurasia (55%) and the Atlantic Coast (13%). As human activity has increased in the Great Lakes watershed, the rate of introduction of exotic species has increased. Almost one-third of the organisms have been introduced in the past 30 years, a surge coinciding with the opening of the St. Lawrence Seaway in 1959. Five categories of entry mechanisms were identified: unintentional releases, ship-related introductions, deliberate releases, entry through or along canals, and movement along railroads and highways. Entry mechanisms were dominated by unintentional releases (29%) and ships (29%). Unintentional releases included escapees from cultivation and aquiculture, bait, aquarium, and other accidental releases. Ship-related introductions included ballast water (63%), solid ballast (31%), and fouling. Introductions via canals represent a small percentage of entries into the Great Lakes. We have identified 13 non-indigenous species (9%) that have substantially influenced the Great Lakes ecosystem, both economically and ecologically. The apparent lack of effects of 91% of the exotic species*

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in the Great Lakes does not mean that they have had little or no ecological impact. Alterations in community structure may predate modern investigations by decades or centuries, and the effects of many species have simply not been studied. As long as human activities provide the means through which future species can be transported into the Great Lakes basin, the largest freshwater resource in the world will continue to be at risk from the invasion of exotic organisms.

INDEX WORDS: Great Lakes, exotic species, non-indigenous flora and fauna, transport vectors.

INTRODUCTION

The rate of dispersal of living organisms and their component genetic material has accelerated with increased anthropogenic activity around the world. Introduced or exotic species, defined as successfully reproducing organisms transported by humans into regions where they did not previously exist, have been brought to new areas of the world for many centuries. The movement of living organisms by aboriginal peoples is well known, ranging from the synanthropic transport of plants and animals by Polynesians across the Pacific Islands to the movement of Mediterranean species by early colonists across the face of Europe. Later, as Europeans began to explore new continents, the influx of non-native species into new regions began and accelerated as technological advancements and development increased. These activities have caused 10-30% of the flora of most regions to be non-native species (Heywood 1989). The success of introduced organisms depends on many factors, including their survivability in unfavorable conditions, adaptability to new environments, high reproductive capability, and their ability to disperse rapidly (Baker and Stebbins 1965). Understanding the effects of introduced species on different ecosystems is critical because successful exotics may render previously stable systems unbalanced and unpredictable. Such global mixing of organisms has contributed to the world-wide loss of diversity in aquatic (Baker and Stebbins 1965) and terrestrial (Heywood 1989) communities.

The Laurentian Great Lakes have been subject to invasion by exotic species since settlement by Europeans. The impacts of some of these species have been enormous. The sea lamprey has cost both millions of dollars in losses to commercial Great Lakes fisheries and millions of dollars in control programs (Fetterolf 1980). The establishment of the zebra mussel, *Dreissena polymorpha,* in the Great Lakes (Hebert *et al.* 1989) poses major economic and ecological threats, costing hundreds of millions of dollars. Zebra mussels are of immediate threat to utilities and industries because they are a major biofouler. There is also concern about the zebra mussel's potential impacts on the structure of freshwater ecosystems as a result of its filter-feeding activities.

Despite the large number of exotics in the Great Lakes, there has been no attempt to prepare a comprehensive list of all known or suspected introduced species. Emery (1985) listed the fish introductions, and workers within other taxonomic groups have identified certain introduced species, but no one has inventoried the entire range of exotic species in the Great Lakes. We present here a comprehensive inventory of the introduced flora and fauna of the Great Lakes. This list includes fishes, invertebrates, aquatic plants, algae, and pathogens that have entered the Great Lakes since the early 1800s. We have attempted to establish the first date of collection and the first recorded locality for each exotic species in the Great Lakes, probable mechanism(s) of introduction, and probable origin. We have not attempted to ascertain the present distribution of each exotic species.

History of Dispersal Mechanisms

In northeastern North America, at least four centuries of European exploration, colonization, and commercial development (Hatcher 1944, Ashworth 1986) have set the stage for biological invasions into the Great Lakes. Long before Europeans arrived, however, invasions and introductions into the Great Lakes probably occurred regularly. As the last Wisconsin glacial ice stage retreated and the Great Lakes were formed between 14,000 and 4,000 years ago (Flint 1971), organisms invaded the basin, making the biological community in the Great Lakes relatively young. Indians living in the region at the time, like the aboriginal peoples of the Pacific and Europe (Heywood 1989), probably transported animals and plants among and into the Great Lakes, beginning a trend that accelerated with European settlement.

The rapid changes that have influenced the Great Lakes for the past four centuries began after the French started colonizing the region in the 17th century. Europeans brought new technology, religion, and conflict into the region and used the basin as a source of furs for their markets. When the French were defeated in the mid-18th century and the English gained control of the Great Lakes, settlers from all parts of Europe arrived, some using the seemingly limitless supply of timber, minerals, and fur-bearing animals to build large businesses that employed thousands of people (Hatcher 1944). Large cities grew around strategic ports where Midwestern grain, ore, lumber, furs, and other products were exported to locations worldwide. The opening of the St. Lawrence Seaway increased trade on the Great Lakes dramatically which in turn increased growth of midwestern port cities. Today, these ports represent 5 of the 15 largest cities in the U.S. and 5 of the 15 largest cities in Canada, attesting to the influence of the Great Lakes as portals to the heart of North America (Ashworth 1986).

During the historical development of the Great Lakes basin, human activities have played a substantial role in the introduction of non-indigenous organisms into the world's largest freshwater resource. These activities, described below, have acted alone or jointly in mediating the introductions of exotic species.

Release (Deliberate)

The early history of deliberate releases of fishes into the Great Lakes is lost in obscurity. DeKay (1842) noted the introduction of common carp into the Hudson River by a "patriotic" citizen and encouraged others to bring fishes from Europe, specifically turbot and sole, for establishment in North American waters. By the early 1870s, deliberate stocking of fish species such as Pacific salmon *(Oncorhynchus* sp.) and common carp *(Cyprinus carpio)* by government fish hatcheries had commenced (Emery 1985). The intentional introduction of native North American mollusks (such as the larger freshwater mussels) into the Great Lakes is not well known, although amateur naturalists were known to have been engaged in such activities throughout North America by at least the mid-nineteenth century. These movements were motivated in part by a perceived desire to increase natural diversity. Kew (1893) for example, noted that a variety of freshwater snails (including *Melantho (=Campeloma), Goniobasis (= Elimia), Somatogyrus, Vivipara (= Viviparus),* and *Bythinia (= Bithynia)* (synonymy from Burch 1989)) were moved by naturalists in the northeastern United States into such localities as the Mohawk River. Erie Canal, and Schuyler's Lake, New York.

Release (Unintentional)

The release of organisms without intention of creating established populations has occurred through a variety of ways. These include:

Release (Aquarium)

The release of aquarium pets into the environment is a practice thought by some to be more humane than other means of disposal. Generally. owners never intended to establish self-sustaining populations of their pets, even though they knowingly released them into favorable habitat (Schmeck 1942).

Release (Cultivation)

The accidental escape of cultivated plants from ornamental gardens and agriculture is a very common mechanism for the introduction of aquatic plants. These introductions have occurred since colonial times when settlers brought over plants to use for medicinal (Torrey 1843 - bittersweet), gastronomical (Green 1962 - water cress), and ornamental purposes (Judd 1953- yellow flag).

Release (Fish)

Release of unused bait by fishermen and transport of fishes from one drainage basin to another in fishing vessels are activities through which fish species are introduced. Rudd, *Scardinius erythrophthalmus,* has been introduced through bait bucket release. Release of disease pathogens (such as the causative agent for furunculosis, *Aeromonas salmonicida* (Bullock *et al.* 1983)) with stocked fish, accidental release of other species of fish with stocked fish (such as the possible introduction of alewife with American shad (Emery 1985)), and introduction of plankton in fish transport water are means through which stocking programs can indirectly and unintentionally introduce organisms.

Release (Accidental)

The accidental introduction of organisms in any other manner is covered under this release mechanism. Examples are the introduction of marine algae into inland brackish habitats from kitchens discarding seafood packaging and shells (Taft 1946), and the accidental release of invertebrates with plants imported for the aquarium trade or ornamental gardens (Goodrich 1911, Aston 1968).

Shipping Activities

The potential for inoculation of the Great Lakes by freshwater organisms from distant drainage basins in North America or from the European continent began in the 1840s and 1850s, with completion of the first passages by ocean-going vessels in and out of the Great Lakes. By the mid- 1840s it was possible to sail from Lake Ontario to Europe (for example the passage of the brigantine *Pacific* in 1844 from Toronto to Liverpool), and by the late 1850s passage from Lake Michigan to Europe had been achieved (for example, the voyage of the steamer *Dean Richmond* from Lake Michigan to Liverpool in 1857) (Mills 1910, LesStrang 1981, Larson 1983). By the early 1860s dozens of vessels were making similar voyages, and presumably many of these were returning from Europe to their home Great Lakes ports. This commerce was facilitated by the completion of: 1) the Welland Canal in 1829, 2) the locks at Sault Ste. Marie in 1855 (permitting complete translake navigation), and 3) the St. Lawrence River canal system in 1847 (permitting vessels to sail from the Great Lakes to the sea). Canals and locks improved steadily throughout the late nineteenth and early twentieth centuries, and ocean commerce expanded considerably.

Ships (Fouling)

Although freshwater fouling organisms from Europe are not likely to survive a transoceanic voyage of several weeks into North America, introduction of fresh and brackish water Atlantic coastal organisms into the basin is possible. Use of the canals for trading between Great Lakes ports and cities on the Hudson or the St. Lawrence provided an opportunity for fouling organisms to be transported upstream into the Great Lakes. The sea lamprey and several species of algae, for example, are thought to have invaded the Great Lakes basin through natural movement upstream through canals and attachment to ships plying these canals.

Ships (Solid Ballast)

Before technological advances enabled humans to use water as ballast, soil, mud, shoreline rocks, sand, and beach debris were often used. When a ship arrived in port to take on cargo, the ballast was dumped onto ballast grounds or thrown overboard (Lindroth 1957). Plants (often as seeds) and invertebrates (particularly insects) were transported in this material across the ocean or inland through canals and deposited in dumping grounds and harbors in the Great Lakes and along the coast. The occurrence of European plants on ballast dumping grounds is well documented (Martingale 1876, Burk 1877, Brown 1879). In New York City, streets were occasionally filled and resurfaced with ballast, and the plants associated with the ballast were then found in relatively high numbers in the reworked area (Brown 1879). Lycopus *europaeus,* European water horehound, was a well documented solid ballast introduction in New York City (Brown 1879). Since similar types of organisms may occur in packaging materials, dunnage, and other in-port releases (such as plants in animal bedding) and in solid ballast, distinguishing between these mechanisms is nearly impossible. Because of this problem, we will include all these mechanisms with solid ballast.

Ships (Ballast Water)

Ballast water was in use by the 1880s and could have been released into the Great Lakes well before 1900 (Carlton 1985). In 1875, work to enlarge canals from the St. Lawrence River to Lake Superior began and continued until they could accommodate a ship 79 meters long with a 13 meter beam and a 4 meter draught (Anonymous 1922). Although the ships were not the enormous vessels seen today in the St. Lawrence Seaway, ballast they brought into the Great Lakes may have been substantial. With the opening of the enlarged Seaway system on 26 June 1959 (Ashworth 1986), the amount of ballast water released into the Great Lakes increased dramatically because of the larger size and increased frequency of ships transiting directly from Europe and other ports of origin through the St. Lawrence Seaway.

Canals

A vast network of canals began to take shape in northeastern North America by the late 1700s. These canal systems connected adjacent watersheds and thus dissolved many of the natural barriers to the dispersal of freshwater organisms into the Great Lakes. The canals may have particularly altered the distributions of animals and plants not likely to have been dispersed by birds or other terrestrial and semiaquatic animals. Organisms like the sea lamprey have used these dispersal corridors to expand into the Great Lakes. Celebrations marking the completion of the Erie Canal in 1825 ironically illustrate the potential impact of the canals on the Great Lakes. For example, on the arrival of the first boats to officially navigate the Erie Canal from Buffalo to New York, the Governor of New York "performed the ceremony of commingling the waters of the Great Lakes with the ocean, by pouring a keg of...Lake Erie (water) into the Atlantic !" (Mills 1910).

Railroads and Highways

The construction of railroads and highways provided several different types of introduction mechanisms. Railroad and highway building creates corridors of continuously disturbed habitat ideal for the movement of introduced plants into new regions and the establishment of new plants introduced with railroad gravel and lumber. The migration of plants along man-made railroad margins is known to have occurred from the Atlantic Coast and from the midwest into the Great Lakes basin.

METHODS

We define exotic species as successfully reproducing organisms transported by humans into the Great Lakes, where they did not previously exist. The following criteria for data collection outline the methods used in this study. These data are included in species tables at the beginning of the individual case histories for each group of organisms. Tables 1 and 2 list the codes for locations and transfer mechanisms used in the species tables (Tables 3 and 4). When a location is not in the Great Lakes proper but in the watershed of a lake, these codes are used to indicate in which lake's watershed the location occurs.

First Date and Location of Collection

The date and location of the first observation of each exotic species in the Great Lakes drainage were largely ascertained from the literature. In some cases, workers did not indicate first sighting of specimens according to date or location but used a broad period (e.g., "1960s") or a general location (e.g., "widespread"). We have, however, always attempted to distinguish between the actual date of first collection and the publication date of the paper first recording an exotic species. In most cases, of course, the first sighting of a species is likely to be sometime after the date at which it gained entry into the Great Lakes. For consistency we have chosen to use the collection dates (if available) rather than speculated dates of introduction. For example, the zebra mussel *Dreissena* was first collected in the Great Lakes in 1988; the specimens were at least 2 years old, but we list 1988, rather than 1986, as the date of record.

TABLE 1. Location abbreviations of exotic species in the Great Lakes.

Location	*Code*
Lake Ontario	O
Lake Erie	E
Lake St. Clair	StC
Lake Huron	H
Lake Michigan	M
Lake Superior	S
tributaries	T

TABLE 2. Codes for transport mechanisms of exotic species entering the Great Lakes.

Mechanism	Code
Release (Deliberate)	R(D)
Release (Unintentional)	R(U)
Release (Aquarium)	R(AQ)
Release (Cultivation)	R(C)
Release (Fish)	R(F)
Release (Accidental)	R(A)
Shipping activities	s
Ships (Ballast Water)	S(BW)
Ships (Solid Ballast)	S(SB)
Ships (Fouling)	S(F)
canals	c
Railroads and Highways	RH

Probable Entry Mechanism(s)

The mechanism or vector of introduction is defined as the most probable means by which a species was introduced into the Great Lakes. We have attempted to identify possible entry mechanisms for each organism, in part based on knowledge of individual species' biology. For some the transport mechanism remains unknown. For many species it is not possible to identify a single mechanism of introduction, and, in these cases, we have discussed several possible entry mechanisms and categorize them under the multiple mechanism.

Geographic Source and Origin of Exotic Species

Although the precise origins of many of the non-native species in the Great Lakes are not known, a broad geographic origin for each species has been determined. In this study, we have identified six different geographic regions of origin including Europe/Eurasia, Asia, North American Atlantic Coast. North American Pacific Coast, Southern U.S., and the Mississippi River drainage system. The Europe and Eurasia origins have been combined here because in many cases authors do not distinguish between these geographic ranges. The native range of an organism, however, may not be the source of the Great Lakes populations of the species. *Corbicula fluminea,* for example, was firmly established in other parts of North America before it was discovered in the Great Lakes. It can be reasonably presumed that the Great Lakes populations of *Corbicula* did not originate in Asia, but from some other part of North America. We have discussed these origins in cases where the invasion history of the exotic species is well known. We have not attempted to document movement of species native to parts of the Great Lakes (such as the threespine sticklebacks, *Gasterosteus aculeatus)* that have expanded their range within the basin (Stedman and Bowen 1985).

RESULTS

Aquatic Fauna

Fish

The fishes (Table 3) are the best studied group of freshwater introduced species in North America. Several publications list the known exotic species of the United States and Canada (Courtenay *et al.* 1984, 1986), Canada (Crossman 1984, 1991), and the Great Lakes (Emery 1985). Other studies have summarized the genetic, ecological, and economic effects of introduced fishes on native species (Christie *et al.* 1972, Berst and Spangler 1973, Hartman 1973, Krueger and May 1991). Additional research has focused on the postglacial dispersal of Great Lakes fishes (Bailey and Smith 1981) and the potential invasion of fishes due to climatic warming (Mandrak 1989). The following discussion will build on Emery's (1985) treatment of Great Lakes introduced fishes and discuss more recently introduced species. The taxonomy of the fishes discussed below is according to Robins *et al.* (1991).

Several fish species have not established self-sustaining populations in the Great Lakes, but have remained consistently abundant due to continued stocking programs. We include these because their impact on the Great Lakes is as substantial, if not more, than most of the established introductions.

Petromyzontidae:
Petromyzon marinus SEA LAMPREY

Because it was not discovered in the Great Lakes until the 1830s in Lake Ontario, the sea lamprey is thought to have migrated through the Erie Canal either from its native habitat in the Atlantic drainage (Emery 1985) or attached to boats plying the Erie and St. Lawrence Canal systems (Morman *et al.* 1980). Another school of thought believes that the sea lamprey is native to the Lake Ontario drainage basin (Lawrie 1970), a possibility Smith (1985) supports because of the discontinuous distribution between the freshwater lamprey populations in the New York Finger Lakes and the Hudson River population. However, DeKay (1842) found the sea lamprey as far upstream in the Hudson River as Albany, New York. The construction and opening of the Erie Canal in the early 1800s probably gave the lamprey a route into the Great Lakes drainage from the Hudson River drainage. The lamprey did not reach Lake Erie until 1921 (Dymond 1922), a delay possibly due to modifications to the Welland Canal in 1881 which altered drainage patterns. Before these alterations, the canal was split into two sections, one draining into Lake Erie and the other draining into Lake Ontario. The Grand River, west of the Welland Canal in Ontario, was used to feed these sections. After 1881, Lake Erie water flowed through the canal directly into Lake Ontario. Ashworth (1986) suggests that fish swimming upstream would have been diverted into the Grand River before the drainage was altered because of their instinct to swim upstream during spawning. When they reached the portion of the canal draining downstream into Lake Erie, they would take the upstream route into the Grand River. Ashworth (1986) also suggests that the final cutting off of the Grand River from the Welland Canal in 1921 could have been the decisive factor in the appearance of the sea lamprey in Lake Erie and its

TABLE 3. Origin, date and location of first sighting, and entry mechanism(s) for non-indigenous aquatic fauna of the Great Lakes. For location and introduction mechanism codes see Tables 1 and 2.

Taxon	Species	Common Name	Origin	Date	Location	Mechanism
Fish						
Petromyzontidae	*Petromyzon marinus*	sea lamprey	Atlantic	1830s	Lake Ontario	C, S(F)
Clupeidae	*Alosa pseudoharengus*	alewife	Atlantic	1873	Lake Ontario	C, R(F)
Cyprinidae	*Carassius auratus*	goldfish	Asia	<1878	widespread	R(D), R(AQ) R(F), R(A)
	Cyprinus carpio	common carp	Asia	1879	widespread	R(D)
	Notropis *buchanani*	ghost shiner	Mississippi	1979	Thames River (StC)	R(F)
	Phenacobius mirabilis	suckermouth minnow	Mississippi	1950	Ohio(E)	C, R(F)
	Scardinius erythrophthalmus	rudd	Eurasia	1989	Lake Ontario	R(F)
Cobitidae	*Misgurnus anguillicaudatus*	oriental weatherfish	Asia	I 939	Shiawassee River (H)	R(A)
Ictaluridae	*Noturus insignis*	margined madtom	Atlantic	1928	Oswego River (0)	C, R(F)
Osmeridae	*Osmerus mordax*	rainbow smelt	Atlantic	1912	Crystal Lake (M)	R(D)
Salmonidae	*Oncorhynchus gorbuscha*	pink salmon	Pacific	1956	Current River (S)	R(A)
	Oncorhynchus kisutch	coho salmon	Pacific	1933	Lake Erie	R(D)
	Oncorhynchus nerka	kokanee	Pacific	1950	Lake Ontario (T)	R(D)
	Oncorhynchus tshawytscha	chinook salmon	Pacific	1873	All Lakes but S	R(D)
	Oncorhynchus mykiss	rainbow trout	Pacific	1876	Lake Huron (T)	R(D)
	Salmo trutta	brown trout	Eurasia	1883	Lakes Ontario (T) and Michigan (T)	R(A) R(D)
Poeciliidise	*Gambusia affinis*	western mosquitofish	Mississippi	1923	Cook Co., Illinois	R(D)
Gasterosteidae	*Apeltes quadracus*	fourspine sticklebacks	Atlantic	1986	Thunder Bay (S)	S(BW)
Percichthyidae	*Morone americana*	white perch	Atlantic	1950	Cross Lake (O)	C
Centrarchidae	*Enneacanthus gloriosus*	bluespotted sunfish	Atlantic	1971	Jamesville Res. (O)	R(AQ), R(F)
	Lepomis humilis	orangespotted sunfish	Mississippi	1929	Lake St. Mary's (E)	C
	Lepomis microlophus	redear sunfish	Southern U.S.	1928	Inland Indiana (M)	R(D)
Percidae	*Gymnocephalus cernuus*	ruffe	Eurasia	1986	St. Louis River (S)	S(BW)
Gobiidae	*Neogobius melanostomus*	round goby	Eurasia	1990	St. Clair River (SW)	S(BW)
	Proterorhinus marmoratus	tubenose goby	Eurasia	I 990	St. Clair River (StC)	S(BW)
Molluska						
Valvatidae	*Valvata piscinalis*	European valve snail	Eurasia	1897	Lake Ontario	S(SB)
Viviparidae	*Ciparsgopaludina chinensis malleata*	Oriental mystery snail	Asia	1931	Niagara River	R(AQ)
	Cipangopaludina japonica		Asia	1940s	Lake Erie	R(D)
	Viviparus georgianus	‘ banded mystery snail	Mississippi	<1906	Lake Michigan (T)	R(AQ)

Continued

TABLE 3. Continued

Taxon	Species	Common Name	Origin	Date	Location	Mechanism
Bithyniidae	*Bithynia tentaculata*	faucet snail	Eurasia	1871	Lake Michigan	S(SB), R(D)
Hydrobiidae	*Gillia altilis*	snail	Atlantic	1918	Oneida Lake (O)	C
Pleuroceridae	*Elimia virginica*	snail	Atlantic	1860	Erie Canal	C
Lymnaeidae	*Radix auricularia*	European ear snail	Eurasia	1901	Chicago (M)	R(AQ), R(A)
Sphaeridae	*Sphaerium corneum*	European fingernail clam	Eurasia	1952	Rice Lake (H/O)	Unknown
	Pisidium amnicum	greater European pea clam	Eurasia	1897	Genesee (O)	S(SB)
Corbiculidae	*Corbicula fluminea*	Asiatic clam	Asia	1980	Lake Erie	R(A), R(AQ), R(F)
Dreissenidae	*Dreissena polymorpha*	zebra mussel	Eurasia	1988	Lake St. Clair	S(BW)
	Dreissena sp.	zebra mussel	Eurasia	1991	Lake Ontario	S(BW)
Unionidae	*Lasmigona subviridis*	mussel	Atlantic	<1959	Erie Canal	C
Crustaceans						
Cladocera	*Bythotrephes cederstroemi*	spiny water flea	Eurasia	1984	Lake Huron	S(BW)
	Eubosmina coregoni	water flea	Eurasia	1966	Lake Michigan	S(BW)
Copepoda	*Eurytemora affinis*	calanoid copepod	widespread	1958	Lake Ontario	S(BW)
	Skistodiaptomus pallidus	calanoid copepod	Mississippi	1967	Lake Ontario	R(A), R(F)
	Argulus japonicus	parasitic copepod	Asia	<1988	Lake Michigan	R(F), R(AQ)
Amphipoda	*Gammarus fasciatus*	gammarid amphipod	Atlantic	<1940	Unknown	S(BW), S(SB)
Oligochaetes						
Naididae	*Ripistes parasita*	oligochaete	Eurasia	1980	North Channel (H)	S(BW)
Tubificidae	*Branchiura sowerbyi*	oligochaete	Asia	1951	Kalamazoo River (M)	R(A)
	Phallodrilus aquaedulcis	oligochaete	Eurasia	1983	Niagara River	S(BW)
Other Invertebrates						
Platyhelminthes	*Dugesia polychroa*	flatworm	Eurasia	1968	Lake Ontario	S(BW)
Hydrozoa	*Cordylophora caspia*	hydroid	Unknown	1956	Lake Erie	R(A)
	Craspedacusta sowerbyi	freshwater jellyfish	Asia	1933	Lake Erie (T)	R(A)
Insects	*Acentropus niveus*	aquatic moth	Eurasia	1950	Lake Ontario, Erie	R(A)
	Tanysphyrus lemnae	aquatic weevil	Eurasia	<1943	Unknown	Unknown
Disease pathogens						
Bacteria	*Aeromonas salmonicida*	furunculosis	Unknown	<1902	Unknown	R(F)
Protozoa	*Glugea hertwigi*	microsporidian parasite	Eurasia	1960	Lake Erie	R(F)
	Myxobolus cerebralis	salmonid whirling disease	Unknown	1968	Ohio (E)	R(F)

subsequent spread to all of the Great Lakes. Sea lamprey predation caused the decline of native lake trout populations in the Great Lakes (Lawrie 1970).

Clupeidae:

Alosa pseudoharengus ALEWIFE

The alewife was discovered in Lake Ontario in 1873 and either expanded through the Erie Canal into the Great Lakes basin from the Atlantic drainage (Emery 1985) or was native to Lake Ontario but was depressed by Atlantic salmon and lake trout until their decline in the late 1800s (Smith 1970). As in the sea lamprey's case, alewife did not expand into Lake Erie until the twentieth century, after alterations were made on the Welland Canal (Ashworth 1986). First records of alewife from Lake Erie were in 1931. Undocumented accidental introductions of alewives with stocked American shad *(Alosa sapidissima)* may have occurred (Emery 1985). DeKay (1842) noted the appearance of alewife with shad in New York coastal waters but noted that alewives were not very abundant compared with the numerous populations found on the Massachusetts coast and in Chesapeake Bay.

Cyprinidae:

Carassius auratus GOLDFISH

Original introductions of the Asian goldfish into North America began as early as the late 1600s and by 1842 goldfish were established in ponds in New York and other nearby states (DeKay 1842). The fish was first officially imported into North America in 1878 when they were propagated in ponds in Washington, D.C. As more fish were propagated, they were distributed to fish hatcheries in Great Lakes states (Jerome 1879) and other parts of the country for use as forage for largemouth bass (Courtenay *et al.* 1984). The original goldfish introductions into the Great Lakes basin probably occurred through bait bucket release. After these initial releases, humans have continued to introduce the fish through direct stocking, escape from or release with fish from hatcheries, release as an unwanted aquarium pet, or escape from private ornamental ponds.

Cyprinus carpio COMMON CARP

The first introduction of the Eurasian common carp into North America was in 1831 when a private citizen imported the fish from France for propagation in his ponds in Orange County, New York (DeKay 1842). For several years, these common carp were released into the Hudson River where they were subsequently caught by commercial fishermen. The fish was not known to be stocked into the Great Lakes basin until after 1879 when the U.S. Fish Commission distributed to Great Lakes states the progeny of fish that were imported from Europe in the 1870s. The fish have since become very abundant, supporting a commercial fishery on Lake Erie and destroying habitat used by more favored fish and waterfowl (Emery 1985).

Notropis buchanani GHOST SHINER

The ghost shiner, a fish native to the Mississippi drainage, was first observed in the Great Lakes drainage in 1979 in abundance in the backwaters of the Thames River (flowing into Lake St. Clair) in Kent County, Ontario (Helm and Coker 198 I). This location is 510 km from the nearest ghost shiner populations and its transfer could have occurred in fishermen's bait buckets with unused bait.

Phenacobius mirabilis SUCKERMOUTH MINNOW

The suckermouth minnow's invasion into the Great Lakes Basin is reviewed by Trautman (1981). The fish is a plains riverine species that favors turbid organically rich streams. It is thought to have been restricted to west of the Mississippi River until 1876 when it was reported from Illinois (Nelson 1876). The fish gradually migrated across Illinois and Indiana until 1920, when it was discovered in Ohio. The migration of the suckermouth minnow parallels the transformation of the natural prairie and forest to farmland by man which converted clear streams with gravel and sandy bottoms to turbid ones with silty bottoms. By 1950, the species was present in Sandusky Bay tributaries. Trautman (1981) observes that it often becomes very abundant in newly invaded areas, but as it becomes established, the population declines. Trautman (1981) also suggests that fishermen using the species as bait may have introduced it into some Ohio Rivers. Like the orangespotted sunfish *(Lepomis humilis), Phenacobius mirabilis* may have entered the Great Lakes basin through Lake St. Mary's, which has a spillway to both Mississippi River and Great Lakes drainages.

Scardinius erythrophthalmus RUDD

The rudd was first introduced from Europe into North America by 1897 when it was discovered in Central Park in New York City (Bean 1897, Bean 1903, and Hubbs 1921). In 1916 the state of Wisconsin deliberately introduced the species into Oconomowoc Lake, Waukesha County, Wisconsin, outside of the Great Lakes drainage (Cahn 1927). This population in Wisconsin, however, did not become permanently established and may have introgressed with the golden shiner, *Notemigonus crysoleucas*, with which it hybridizes (Burkhead and Williams 1991). In 1936 it was established in the Roeliff-Jansen Kill in eastern New York southeast of Albany near the Massachusetts border (Smith 1985) and in the early 1950s, the first rudd from the Great Lakes drainage basin was collected in Cascadilla Creek near Ithaca, New York (Courtenay *et al.* 1984). In recent years, it has been cultured in Arkansas for use as a preferred hardy bait fish similar to golden shiners. Fisheries biologists were not alerted to the spread of rudd until it had been distributed to bait dealers for several years (Burkhead and Williams 1991). In 1989, rudd were discovered in Lake Ontario and the St. Lawrence River (J. Farrell, SUNY College of Environmental Science and Forestry, personal communication 1990) and in 1990, an established population was discovered in Oneida Lake, New York, in the Lake Ontario drainage (J. Forney and D. Green, Cornell University Biological Field Station, personal communication, 1990).

Cobitidae:
Misgurnus anguillicaudatus ORIENTAL WEATHERFISH

An aquarium supply facility in Michigan first imported the Oriental weatherfish into the Great Lakes drainage in 1939 and propagated them in a pond in the Shiawassee River drainage basin, which drains into Saginaw Bay, Lake Huron (Schultz 1960). The escape of the fish was first discovered in 1958 when the Michigan Department of Conservation found them in a private pond that drained into the same stream as the aquarium supply facility's pond. Establishment of the fish probably occurred shortly after its importation in 1939 and its spread from the point of introduction began soon after. Surveys of the Shiawassee River in 1958 and 1959 showed the fish established in a number of localities in the headwaiters of the river (Schultz 1960).

Ictaluridae:
Noturus insignis MARGINED MADTOM

The margined madtom, native to Atlantic drainages, was first reported in the Great Lakes drainage in 1928 in the tributaries on the southern shores of Lake Ontario (Emery 1985). The presence of this fish in these rivers is likely due to the diversion of a Susquehanna stream into the Oswego River drainage. A common bait fish, the margined madtom has also been found in inland areas in Michigan's upper peninsula and in parts of the Lake Ontario watershed.

Osmeridae:
Osmerus mordax RAINBOW SMELT

The earliest known record of rainbow smelt in the Great Lakes basin is from Michigan, where they were stocked in 1912 in Crystal Lake, Michigan, which is in the Lake Michigan drainage (Van Oosten 1937). Although earlier plantings of this species are known from the St. Marys River in 1906, the planting in Crystal Lake is considered the source for the upper Great Lakes populations of rainbow smelt. However, origin of Lake Ontario populations has been debated. These populations are thought to have either been native to the lake or have migrated up the Erie Canal system from the Atlantic drainage. DeKay (1842), however, only noted rainbow smelt from coastal areas and does not record it from the upper Hudson River. At the time, the species was economically valuable in coastal markets. This coastal distribution suggests that rainbow smelt populations in the Lake Ontario basin in central New York are either not native or that they were overlooked in early surveys.

Salmonidae:
Oncorhynchus gorbuscha PINK SALMON

Pink salmon, a native of the west coast, was introduced into Lake Superior and the Current River, in 1956. The introductions resulted from activities of a stocking program to introduce pink salmon into Hudson Bay and occurred at the Port Arthur Fish Hatchery in Ontario. Although several different releases occurred, the disposal by hatchery managers of excess stock, about 21,000 fingerlings. into the Current River after the Hudson Bay stocking program had been completed, is probably the source of the Great Lakes pink salmon population. It was believed from knowledge of the reproductive biology and ecology of the species that these fingerlings would not establish reproducing populations in Lake Superior. In addition to the excess stock, other introductions occurred at the hatchery either as escapees during the transfer of fish to planes for transport to James Bay or as accidental releases into Lake Superior with the stocking of lake trout fingerlings. Since these original introductions, the population of pink salmon has successfully reproduced and has spread to all the Great