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Research Completion Report *

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

by

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I. Abstract

The objective of this study was to document, through literature review, the introductions of non-indigenous aquatic flora and fauna in the Great Lakes basin since the early 1800s. This documentation includes the date and locality of the organism's first discovery in the Great Lakes basin, the means through which it entered the Great Lakes, and its native range or origin.

The Laurentian Great Lakes have been subject to invasion by exotic species since the settlement of the region by Europeans. Since the 1800s, 136 non-indigenous aquatic organisms have become established in the Great Lakes. The bulk of these organisms have been represented by plants (61), fish (24), algae (24), mollusks (9) and oligochaetes (7). Most of these species have come from Europe (47%), the Atlantic Coast (18%) and Eurasia (14%). As human activity has increased in the Great Lakes watershed, the rate of introduction of exotic species has increased. Over 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. The most commonly utilized entry mechanisms were unintentional releases (37%) and ships (32%). Unintentional releases included escapees from cultivation, accidental releases, releases associated with fish or bait and aquarium releases. Ship related introductions included ballast water (56%), solid ballast (34%) and fouling. Entries through canals represent a small percentage of entries into the Great Lakes.

We have identified 14 non-indigenous species (10%) that have significantly influenced the Great Lakes ecosystem, both economically and ecologically. 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.

II. Introduction

The rate of dispersal of living organisms and their component genetic material has accelerated with increased anthropogenic activity around the world. Exotic species, defined as successfully reproducing organisms transported by humans into regions where they did not exist in historical times, have been introduced into 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 resulted in a 10-30% proportion of non-native species in the floras of most regions (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 Lake 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. The control costs associated with the zebra mussel in the Great Lakes alone have been estimated at $5 billion over 10 years (J. Stanley, U. S. Fish and Wildlife Service, personal communication, 1989). The mussels are of immediate threat to utilities and industries because they are a major biofouler. There is also concern about potential impacts on the structure of freshwater ecosystems, chiefly through 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 introduced species, but none 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 fish, invertebrates, aquatic plants, algae and pathogens that have entered the Lakes since the early 1800s. We have included several unsuccessful introductions and native species previously considered introduced but now thought to be native as well. 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.

III. 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 the Europeans arrived, however, invasions and introductions into the Lakes probably occurred regularly. The Great Lakes were formed during the retreat of the last Wisconsin ice advance. As the ice retreated and the 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. The Indians living around the Lakes at the time, like the aboriginal peoples of the Pacific and Europe (Heywood 1989), probably transported animals and plants among and into the Lakes, dissolving any "natural" biotic patterns that may have given any of the Lakes a unique faunistic or floristic fingerprint.

After the French "discovered" the Great Lakes in the 17th century, the rapid changes that have influenced the Lakes for the past four centuries began. The French brought new technology, religion and conflict into the region and used the basin as a source of furs for European markets. When the French were defeated in the mid-18th century and the English gained control of the Lakes, settlers 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 the strategic ports where midwestern grain, ore, lumber, furs, and other products were exported to locations worldwide. The opening of the St. Lawrence Seaway increased the trade on the Lakes dramatically which in turn increased the growth of the Great Lakes port cities. Today, Great Lakes ports represent five of the fifteen largest cities in the U.S. and five of the fifteen largest cities in Canada, attesting to the influence of the Lakes as portals to the heart of America (Ashworth 1986).

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

Release (Deliberate)

The early history of deliberate releases of fish into the Great Lakes is lost in obscurity. By the early 1870s deliberate stocking of fish species from the Pacific and Europe 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 at least in part by a perceived need to improve natural patterns of diversity. Kew (1893) for example, notes that a variety of freshwater snails (including *Melantho* (= *Campeloma*), *Goniobasis*, *Somatogyrus*, *Vivipara* (= *Viviparus*), and *Bythinia* (=*Bithynia*) (synonymy from Burch 1989)) were moved by naturalists in the northeast United States, into such localities as the Mohawk River, Erie Canal, and Schuyler's Lake, New York.

Release (Unintentional)

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

1. *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).

2. *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 been occurring since colonial times when settlers brought over plants to use for medicinal (Torrey 1843-

bittersweet), gastronomical (Green 1962-watercress) and later for ornamental purposes (Judd 1953-yellow flag). Normally, when the plants were cultivated, they were not intended to spread from the area where they were planted.

3. *Release (Fish)*

The release of unused bait by fishermen and the transport of fish from one drainage to another in fishing vessels are activities through which fish could be introduced. The release of disease pathogens with fish, the accidental release of other species of fish with stocked fish, and the introduction of plankton in the transport water of fish are means through which stocking programs can indirectly and unintentionally introduce organisms.

4. *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 the 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 the 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 and 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 in 1847 of the St. Lawrence River canal system, permitting vessels to sail from the

Great Lakes to the sea, and by the completion in 1855 of the locks at Sault Ste. Marie, permitting complete translake navigation. Canals and locks improved steadily throughout the late nineteenth and early twentieth centuries, and ocean commerce expanded considerably.

1. *Ships (Fouling)*

Although freshwater fouling organisms from Europe are not likely to survive a transoceanic voyage of several weeks into North America, the introduction of fresh and brackish water Atlantic coastal organisms into the basin is possible. The 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, in addition to following canals for natural movement upstream, attached to ships for rapid upstream dispersal into new territory.

2. *Ships (Solid Ballast)*

Before technological advances enabled man to use water as ballast, soil, mud, shoreline rocks and 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 (Martindale 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). 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.

3. *Ships (Ballast Water)*

Ship's ballast water was in use by the 1880s (Carlton 1985) and could have entered the Lakes well before 1900. In 1875, work to enlarge the canals from the St. Lawrence River to Lake Superior began and continued until they could accommodate a ship 260 feet long with a 44-foot beam and a 14-foot draught (Anonymous 1922). Although the ships were not the enormous vessels seen today in the seaway, the ballast that they brought into the Lakes may have been significant. With the opening of the enlarged Seaway system on June 26, 1959 (Ashworth 1986), the amount of ballast water released into the Lakes increased dramatically because of the larger size and 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. The 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 corriders to "naturally" 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 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 corriders of continuously disturbed habitat ideal for plant introductions with gravel and lumber, and movement of introduced plants into new regions. 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.

Saline Habitat

Heavily industrialized areas, urban areas, and areas around salt mines and processing plants have created polluted, saline marshlands in the Great Lakes region (Muenscher 1927, Catling and McKay 1980). This alteration of natural habitat has enabled coastal species to become established (through various transport mechanisms) into areas where they previously would not have succeeded (Farwell 1916). When road salt became widely used as a deicing agent on highways, the roads became favorable habitat for Atlantic coastal marsh species to migrate inland.

The input of road salt and industrial waste into the Great Lakes has also changed the salinity of the lower Lakes to three times their concentration in the 1850s (Sheath 1987). Sheath (1987) asserts that these changes in concentrations have facilitated the introduction of marine algae and its adaptation to freshwater environments.

IV. Criteria for Data Collection

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. The codes used in the species tables for the transfer mechanisms and locations are listed in Tables 1 and 2. Table 1 lists codes used for the Lakes in the tables. 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 ascertained from the literature. In some cases, workers did not indicate first sitings of specimens according to date or location but use 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 or observation of a species and the date of publication of the paper first recording an exotic species. In most cases, of course, the first siting of a species is likely to be sometime after the date at which it gained entry into the 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 found in the Great Lakes in 1988; the specimens were at least two years old, but we list 1988, rather than 1986, as the date of record.

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 each possibility.

Geographic 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 eight different goegraphic regions of origin including Europe, Asia, Eurasia, North American Atlantic Coast, North American Pacific Coast, Southern U.S., Midwestern U.S., and the Mississippi River drainage system. We have not attempted to document movement of native species (such as the threespine stickleback, *Gasterosteus aculeatus* (Stedman and Bowen 1985)) that have expanded their range within the Great Lakes basin.

V. Inventory of Introduced Species

A. Fish

The fish (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), Canada (Crossman 1984) and the Great Lakes (Emery 1985). Other studies have summarized the effects of introduced fish on native species genetically (Krueger and May 1991), ecologically (Christie et al. 1972 and Hartman 1973) and economically. Others have studied the postglacial dispersal of Great Lakes fish (Bailey and Smith 1981) and the potential invasion of fish due to climatic warming (Mandrak 1989). Because Emery's (1985) treatment of Great Lakes introduced fish covers the topic in great detail, the following discussion will build on and review some of his findings in addition to discussing the more recently introduced species.

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

Petromyzontidae:

Petromyzon marinus SEA LAMPREY

Because it was not found in the Great Lakes until the 1830s in Lake Ontario, the sea lamprey is thought to have moved up the Erie Canal 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). The lamprey did not reach Lake Erie until 1921 (Emery 1985). One potential explanation for this delay is suggested by Ashworth (1986), who notes that work done on the Welland Canal in 1881 altered drainage patterns of the canal. 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.

Clupeidae:

Alosa pseudoharengus ALEWIFE

The alewife was discovered in Lake Ontario in 1873 and is also thought to have expanded through the Erie Canal into the Great Lakes basin from the Atlantic drainage (Emery 1985). As in the sea lamprey's case, the alewife did not expand into Lake Erie until the 20th century, after the alterations were made on the Welland Canal (Ashworth 1986). The first records of the alewife from Lake Erie were in 1931. Undocumented accidental introductions of the alewife with stocked American shad may have occurred (Emery 1985). Records of the alewife's migration up the Erie Canal are thought to exist, but remain undiscovered to date.

Salmonidae:

Oncorhynchus gorbuscha PINK SALMON

Pink salmon, native to the west coast, were accidentally introduced in 1956 into the Great Lakes in a Lake Superior tributary, the Current River (Emery 1985). The fish (21,000 fingerlings), were excess stock from an Ontario Department of Lands and Forests release program in Hudson Bay. The fish were released into a sewer that drained into the Current River. The fish has formed a successfully reproducing population in the Great Lakes that has not needed supplementation with stocking.

Oncorhynchus kisutch COHO SALMON

Although it may have been accidentally introduced earlier, the coho salmon was first intentionally stocked into the Great Lakes in 1933 when the Ohio Division of Conservation released them into Lake Erie (Emery 1985). These fish, native to the west coast, survived but did not establish a reproducing population. In 1966, Michigan and Ohio stocked coho salmon which established naturally reproducing populations. Currently, this low level of natural reproduction is supplemented by stocking to enhance the sport fishery.

Oncorhynchus nerka KOKANEE

The first introduction of kokanee, native to the west coast, into the Great Lakes occurred in 1950 when New York stocked Lake Ontario tributaries (Emery 1985). In 1964-72 stocking programs introduced the fish into Lakes Ontario and Huron which resulted in naturally reproducing populations. After the program was discontinued, the population dwindled to the very small numbers that currently persist in Lake Huron and spawn in streams on Manitoulin Island.

Oncorhynchus tshawytsch CHINOOK SALMON

The chinook salmon, a fish native to the west coast, was first introduced into the Great Lakes basin in 1873 when it was stocked into all the Lakes but Lake Superior (Emery 1985). Until 1933, the Great Lakes states tried to establish reproducing populations in the Lakes, but were unsuccessful. More recently, since 1967, chinook salmon have been stocked to support a sport fishery on the Lakes. Studies in Lake Michigan tributaries have estimated that the natural reproduction of these plants has contributed an estimated 23% of the total chinook salmon population in Lake Michigan (Carl 1982).

Oncorhynchus mykiss (=*Salmo gairdneri*) RAINBOW TROUT

Western rainbow trout have been stocked in the Great Lakes since 1876 when they were planted in a tributary to Lake Huron (Emery 1985). Rainbow trout do reproduce in the Lakes, but continued stocking is necessary to support the sport fishery.

Salmo trutta BROWN TROUT

German brown trout were first stocked into the Great Lakes in 1883 when Michigan stocked the Pere Marquette River, a Lake Michigan tributary (Emery 1985). In the same year, an accidental release occurred in the Genesee River, a tributary to Lake Ontario, from a fish hatchery in Caledonia, New York. Stocking of the brown trout continued after these initial attempts and some tributary populations were established. Currently, stocking supplements the sport fishery for brown trout.

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, in the Lake Michigan drainage (Emery 1985). Although earlier plantings of this species are known from the St. Mary's River in 1906, this planting is considered the source for the upper Lakes populations of rainbow smelt. The origin of Lake Ontario populations has been debated. The Lake Ontario populations are thought to have either been native to the lake or have migrated up the Erie Canal system from the Atlantic drainage.

Cyprinidae:

Carrassius auratus GOLDFISH

The history of Eurasian goldfish introductions into the Great Lakes basin is not clear (Emery 1985). The earliest known introduction of the fish into North America was in 1878 when they were imported for propagation in ponds in Washington D.C. As more fish were propagated they were distributed into other parts of the country, but where or when stocking activity occurred is unknown. Since the species is a very popular aquarium fish it probably gained access to the Great Lakes fairly early from direct stocking, as an unwanted aquarium pet or as an escapee from private ornamental ponds.

Ctenopharyngodon idella GRASS CARP

The Asian grass carp was first imported into North America by the U.S. Fish and Wildlife Service for a research program on aquatic plant control in Alabama. Because the fish did not provide the expected solution to aquatic plant problems and many feared that it would become a widespread problem much like the common carp, many states banned its importation. Many private pond owners and golf course owners, however, introduced the fish illegally into ponds throughout the Great Lakes states. In Wisconsin and Michigan, the fish were stocked in 1974 (Emery 1985). These fish are thought to have been obtained from a distributor in Arkansas (E. Woltmann, New York State Department of Environmental Conservation, personal communication, 1990). Since some states made the sale of sterile hybrids of the fish legal, before the distributor of fertile fish was caught, the occasional grass carp found in the Lakes was thought to be sterile. In 1985, specimens were found in Lake Erie near Point Pelee in Canadian waters and in Ohio at the mouth of the Toussaint River (Crossman et al. 1987). Since 1985, the grass carp has been recorded from Lake Ontario near Rochester, New York, Western Lake Erie, Lake St. Clair (Crossman et al. 1987) and Lake Michigan (R. Horner, Illinois Dept. of Cons., personal Communication, 1990). Established populations of grass carp are now present in the Great Lakes.

Cyprinus carpio COMMON CARP

The first introductions of the Eurasian common carp into North America was in 1831 when a private citizen imported the fish for propagation and distribution as an easy food fish (Emery 1985). The fish was not known to be stocked into the Lakes basin until after 1879 when the U.S.

Fish Commission distributed the progeny of imported fish into Great Lakes states. 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 is a fish native to the Mississippi drainage that 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 (Holm and Coker 1981). Its location and abundance suggest that it was introduced as or with bait fish.

Scardinius erythrophthalmus RUDD

The rudd was first introduced into North America in 1916 when the state of Wisconsin deliberately introduced the species into Oconomowoc Lake, Waukesha County, Wisconsin outside of Great Lakes drainage (Cahn 1927). In 1936 it was established in the Roeliff-Jansen Kill in eastern New York southeast of Albany near the Massachussets border (Smith 1985). In recent years, it has been imported from Europe for use as a preferred hardy bait fish substitution for golden shiners (D. Jennings, U. S. Fish and Wildlife Service, personal communication 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 Lake Ontario drainage (J. Forney and D. Green, Cornell University Biological Field Station, personal communication, 1990). The fish is probably currently distributed sporadically in the Great Lakes basin.

Cobitidae:

Misgurnus anguillicaudatus ORIENTAL WEATHERFISH

The Oriental weatherfish was first brought into the Great Lakes basin in 1939 by an aquarium supply house and escaped into the Shiawassee River, which drains into Saginaw Bay, Lake Huron, where it was discovered in 1958 (Emery 1985). The fish likely still persists in the river but has not been reported in other Great Lakes waters (Emery 1985).

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 other parts of the Lake Ontario watershed.

Poeciliidae:

Gambusia affinis WESTERN MOSQUITOFISH

A native of the Mississippi drainage, the moquitofish has been widely stocked in ponds for mosquito control (Krumholz 1944, 1948, Emery 1985). After its introduction in 1923 into the Great Lakes basin in Cook County Illinois, it became established in several parts of Cook County as well as in parts of Michigan, Wisconsin, Ohio, New York, and Ontario (Krumholz 1944, 1948, Emery 1985).

Gasterosteidae:

Apeltes quadracus FOURSPINE STICKLEBACK

Holm and Hamilton (1988) reviewed the introduction of this estuarine species (native to the lower St. Lawrence) into Lake Superior. A reproducing population was first found in 1986 in Thunder Bay, Lake Superior. They note that, because the nearest occurrence of the fish to the Lake Superior population is about 2100 km away in Quebec near the mouth of the Batiscan River, the most likely mechanism of introduction is through ship's ballast water.

Moronidae:

Morone americana WHITE PERCH

The white perch, native to the Atlantic drainage, was first observed in the Lake Ontario watershed in 1950 in Cross Lake in central New York (Dence 1952). The fish is thought to have reached the Lakes through the Mohawk River Valley and the Erie Barge Canal from expanding Hudson River populations (Scott and Christie 1963). It has become an important sport and commercial fish in Lakes Ontario and Erie (Emery 1985).

Centrarchidae:

Lepomis humilis ORANGESPOTTED SUNFISH

The orangespotted sunfish, a native of the Mississippi drainage, was first found in the Great Lakes basin in 1929 in Lake St. Mary's, Ohio (Lake Erie drainage) (Emery 1985). It expanded into Lake Erie tributaries in northern Ohio and southeastern Michigan. It is unknown how *Lepomis humilis* entered the Great Lakes.

Lepomis microlophus REDEAR SUNFISH

Indiana first brought the redear sunfish, native to the southern U.S., into Great Lakes drainage in 1928 (Emery 1985). The fish was stocked into lakes and streams in the northern part of the state. It has since been widely and successfully introduced into inland areas of the basin but reproducing populations have not been observed in the Great Lakes.

Percidae:

Gymnocephalus cernuus RUFFE

The ruffe, a European species, was first collected in the Great Lakes in 1986 in the St. Louis

River, a tributary of Lake Superior and a major harbor for Duluth, Minnesota, and Superior, Wisconsin. The fish probably entered the river in the ballast water of grain ships arriving to pick up cargo (Pratt 1988, Simon and Vondruska 1991). By the summer of 1988 ruffe were clearly established in the St. Louis River. By 1991, the ruffe had become the second most abundant fish in the St. Louis River (J. Selgeby, U. S. Fish and Wildlife Service, personal communication 1991). The abundance of the ruffe in the St. Louis River indicates that its spread into the lower Lakes is probable. As it spreads, the ecological problems the ruffe could bring to systems disturbed by the zebra mussel and other exotics could be significant.

Gobiidae:

Neogobius melanostomus ROUND GOBY

This Eurasian benthic species was first observed in North America in July of 1990 when it was caught by anglers in the St. Clair River near Sarnia, Canada (Jude et al. Unpublished). The fish was most likely transported to the Great Lakes in the ballast water of ships from its native range in the Black or Caspian Seas. The species has established a reproducing population in the St. Clair River and is likely to expand its range into the other Great Lakes.

Proterorhinus marmoratus TUBENOSE GOBY

The Eurasian tubenose goby was first observed in North America in April of 1990 in the St. Clair River where it was collected from the travelling screens of a power plant. It was most likely transported to the river in the ballast water of ships entering the Lakes from Caspian or Black Seas. Interestingly, even though this benthic species is endangered in its native European range, it has become established in the St. Clair River and will likely expand its range further into the Great Lakes basin (Jude et al. Unpublished).

B. Mollusks

The molluscan fauna of the Great Lakes has been studied since the late 1800s when many residents of the region were amateur conchologists (Robertson and Blakeslee 1948). Professional conchologists had identified the mollusks of the Lakes by the late 1800s (Baker 1902), so when a European species was discovered, it was generally correctly identified as introduced. The nonindigenous mollusks of the Great Lakes (Table 4) have entered through mechanisms ranging from ship's ballast to aquarium releases.

Class: Gastropoda

Lymnaeidae:

Radix auricularia EUROPEAN EAR SNAIL

Baker (1901a) first reported *Radix auricularia*, a Eurasian aquarium snail (Robertson and Blakeslee 1948), in North America. In 1901, a high school biology teacher found the snail at Chicago's Lincoln Park, and brought it to Baker's attention. Baker reasoned that since the snail was first found in a propagating greenhouse, it was likely introduced with plants that had just been imported from Belgium. Soon after its first discovery, it was found in a heated ornamental pond in Lincoln Park. Other early Great Lakes records are in Lake Erie (Allen 1911, Goodrich 1911 and Robertson and Blakeslee 1948) and Western Lake Ontario (Latchford 1930). Goodrich (1911) also noted that the snails he found, in a stream 30 meters from Lake Erie were located in the vicinity of greenhouses. He proposed that the snail's eggs were imported into the greenhouses on azaleas from Holland and Belgium and washed into the stream through the drains. Robertson and Blakeslee (1948) note that the snail is a popular aquarium snail, suggesting a second entry mechanism. The snail's current "scattered" (Pennak 1989) and "spotty" (Burch 1989) distribution pattern and the nature of its transport mechanisms, support the probability of multiple, widespread introductions into North America.

Viviparidae:

Debate regarding the taxonomy of two species of viviparid snails, *Cipangopaludina chinensis malleata* and *Cipangopaludina japonica*, centers around whether they should be treated as separate species. Burch (1989) discusses them separately but acknowledges their questionable taxonomy and Clarke (1981b) regards them as synonyms. Since the taxonomy of these snails remains unclear, they will be considered at the generic level in this study.

Cipangopaludina chinensis malleata ORIENTAL MYSTERY SNAIL

Cipangopaludina japonica

In San Francisco, around 1892, the first live specimens of Japanese *Cipangopaludina* were imported for sale in a Chinese market (Wood 1892). The snails, a species commonly consumed in Asia, soon became established in parts of California (Clench and Fuller 1965). Whether these snails were stocked purposely for cultivation or released accidentally (e.g. with unwanted kitchen waste) is unknown. In the Great Lakes, the first known release of the snail occurred in the Niagara River. In 1942 Eugene H. Schmeck found a well established population of *Cipangopaludina chinensis malleata* in the Niagara River at Cayuga Island. Schmeck suggests that his pair of aquarium specimens, which had been breeding when he lived on the island in 1931, were "inadvertently" released into the Niagara River and reflects an actual documentation of the establishment of a species through aquarium release (Schmeck 1942, Robertson and Blakeslee 1948). Another early introduction of these snails into the Great Lakes occurred in Sandusky Bay, Lake Erie, Ohio in the 1940s, when a bushel of *Cipangopaludina japonicus* was supposedly introduced to feed channel catfish (Wolfert and Hiltunen 1968). As they reached high densities in Sandusky Bay, fishermen often made seine hauls containing "two tons" of snails (Wolfert and Hiltunen 1968). Widely distributed in the United States, the snail's 1965 Great Lakes distribution included isolated populations in Michigan and Indiana and abundant populations along the Ohio shoreline of Lake Erie (Clench and Fuller 1965).

Valvatidae:

Valvata piscinalis EUROPEAN VALVE SNAIL

This European snail was first observed in North America in Lake Ontario near the mouth of the Genesee River. The collection occurred at Charlotte and Summerville, New York in 1897 (Baker 1898) and several years later the snails had reached high densities (Baker 1900). The snail was probably introduced with "straw and marsh grass" packaging used in ships transporting "fragile articles" or "crockery" from England and Eastern Europe (Latchford 1914, 1925). Latchford had first observed the snails among packaging debris along the Lake Ontario shore in Toronto in 1912 (Latchford 1930). Since then, the snail has spread through the lower Lakes where it remains common (Burch 1989, Oughton 1938, Dundee 1974).

Bithyniidae:

Bithynia tentaculata FAUCET SNAIL

The earliest observations of *Bithynia tentaculata*, the European faucet snail, in the Great Lakes are from Lake Michigan in 1871 (Robertson and Blakeslee 1948). Believed to have been introduced about 1870 (Berry 1943), it spread rather quickly into all the other Great Lakes except Lake Superior (Baker 1928). *Bithynia* was documented in Lake Ontario at Oswego, New York in 1879 (Beauchamp 1880) and by 1918 the snail had reached the Hudson River (Baker 1928). By 1927 it had been found in the Potomac River at Alexandria, Virginia (Pilsbry 1932, Marshall 1933). Several explanations for the snail's occurrence in the Great Lakes have been proposed. Kew (1893) described the introduction of *Bithynia tentaculata* and several other snails into the Erie Canal, the Mohawk River, and Schuyler's Lake by amateur naturalists. The snail is also thought to have been introduced in either the marsh grass used in packaging crockery and other goods brought into the Great Lakes (Latchford 1914, 1925) or the ballast of timber ships that had direct routes between Lake Michigan ports and Europe (Baker 1928). In the early 1900s, *Bithynia* began infesting municipal water supplies, from the intake pipes to household faucets (Baker 1902), thus giving rise to the snail's common name. In some cases, these fouling problems reached very large proportions. In Erie, Pennsylvania, the water supplies became so infested that "wagon loads" of snails were removed from municipal water pumping stations (Sterki 1911). Although fossil forms of *Bithynia* are present in Pleistocene deposits near Lake Michigan, modern day populations are descendants of the nineteenth century introduction (Baker 1928). Today, *Bithynia* remains abundant in the Great Lakes system (Dundee 1974, Burch 1989).

Class: Pelecypoda

Sphaeriidae:

Sphaerium corneum — EUROPEAN FINGERNAIL CLAM

Herrington (1962) suggested that the clam was "recently" introduced from Eurasia and all distribution information is based on specimens that he personally studied. The clam has been sighted in Lake Champlain, Lake Erie, Lake Ontario, St. Lawrence River, Bay of Quinte, and Rice Lake (Herrington 1962). Rice Lake is a part of the Trent-Severn Canal system, a shallow canal system connecting Lake Huron and Lake Ontario that caters mostly to recreational boat traffic (Ashworth 1986). The introduction mechanism for this clam is unknown.

Pisidium amnicum — GREATER EUROPEAN PEA CLAM

Baker (1898) first found this clam in Lake Ontario at Charlotte and Summerville, New York near the mouth of the Genesee River in 1897 and reported it as *Pisidium bakeri*, a new species that was to have been described by H.A. Pilsbry. Later, however, Sterki informed Baker (1900), of the possibility of synonymy between the Eurasian-African *P. amnicum* and the newly discovered *P. bakeri* , a synonymy that Sterki (1916) confirmed. It is widespread in the eastern Great Lakes, in the St. Lawrence River, Lake Champlain, Pennsylvania and New Jersey (Herrington 1962 and Burch 1975). The clam is thought to have been introduced through shipping activities into Lake

Ontario.

Corbiculidae:

Corbicula fluminea ASIATIC CLAM

The history of the Asiatic clam invasion into the waters of the United States is well documented (McMahon 1982, Counts 1986). It was first observed in North America in British Columbia in 1924 when dead specimens were collected (Counts 1981). The first live collections occurred in 1938 in Pacific County, Washington on the banks of the Columbia River (Burch 1944). The clam steadily spread down the west coast and then into the southern United States (McMahon 1982, Counts 1986) reaching densities in some areas sufficient to damage and clog water intake systems (Clarke 1981a). Until it was collected in Monroe County, Michigan in western Lake Erie in 1980, it was limited to a warmer southern distribution by its intolerance to temperatures of 2 C and lower (Clarke 1981a, McMahon 1982, Scott-Wasilk et al. 1983, Sickel 1986). The invasion of the clams into western Lake Erie has been estimated to have occurred in 1978 and collections have been primarily associated with heated effluent in industrial areas (Scott-Wasilk et al. 1983). White et al. (1984) reported the clam from southeastern Lakes Michigan. Like those found in western Lake Erie, these clams were associated with heated discharge from a power plant. Counts (1986) reviews the dispersal mechanisms of the clam, including byssal attachment to debris and boats, transport by birds, accidental transport with sand or gravel, and release as bait or as aquarium specimens. The clam does have a short planktonic larval stage (Counts 1986) that makes transport in ballast possible. Any of these mechanisms could have introduced the Asiatic clam into Great Lakes waters.

Dreissenidae:

Dreissena polymorpha ZEBRA MUSSEL

Dreissena polymorpha, a European fresh and brackish water mussel, was first discovered in

North America in Lake St. Clair in June 1988 (Hebert et al. 1989). The first confirmed sighting in the western basin of Lake Erie was in July 1988, and by 1991, it was found on the southern shore of Lake Ontario, in the upper St. Lawrence River, along the Erie Canal to just east of Rochester, New York, in Oneida Lake, New York, in the Hudson River and in the Illinois River (New York Sea Grant 1990, E.Mills, Cornell University, personal communication 1991, R. Sparks, Illinois Natural History Survey, personal communication, 1991). The mussel arrived in the ballast water of transoceanic ships from Europe. Ballast transport and fouling can also be credited with the sporadic occurrence at major upper Great Lakes ports in 1990 (New York Sea Grant 1990). The mussel often occurs in very large numbers (Mackie et al. 1989), and can exert large and far-reaching impacts on freshwater ecosystems through biofouling and filter-feeding. Reaching high densities in parts of Lake St. Clair, the mussels have been shown to detrimentally effect the native unionids in the lake and to improve water quality in the Detroit River (Hebert et al. 1991).

Mollusks previously thought to be introduced but now considered native.

Pisidium henslowanum HENSLOW'S PEA CLAM

The first records of this European clam in North America resulted from specimens collected in a British land exploration expedition by John Richardson (1836). Richardson found the clam from "Lake Superior to Lake Winnipeg" and gave the specimens (along with all the other mollusks collected) to British mollusc expert James Sowerby for identification in 1828. These early records were long regarded as misidentifications, since the clam was not found again in North America until the early 1900s, over 70 years later, in Lake Ontario (Dall 1905). Dall (1905) lends credibility to the early records because of Sowerby's expertise and because the Lake Ontario records showed that the clam did indeed have a North American distribution. Sterki (1916) cites Richardson's (1836) distribution from Dall (1905) and adds a Lake Champlain record. He calls the clam "palearctic" and "nearctic" in distribution. Herrington (1962), reviewing the previous records, noted the possibility of the clam being an introduction into the Great Lakes and added new records from Lake Michigan, Lake Ontario, and the St. Lawrence River. Harris (1973) reviewed the literature on the species and reported new records from Alberta, British Columbia, Manitoba and Ontario. He concludes that it is a "widespread boreal species ranging from the northern United States almost to the Arctic Circle." This distribution is supported by the presence of fossil forms in Idaho (Herrington 1962) and in 7000 year old post glacial deposits (Harris 1973).

Pisidium supinum HUMP-BACKED PEA CLAM

Sterki (1916) reported this clam as a "rare" inhabitant of palearctic and nearctic areas and cites records from Lake Ontario. More recent reports of the clam are from eastern Lake Ontario and the Ottawa River in 1959 (Herrington 1962, Clarke 1981b) and from the Eastmain and LaGrande Rivers which drain into Hudson Bay (Clarke 1981b). The new distribution information, along with fossil records from the Pliocene and Early Pleistocene in Idaho, indicate that the clam is probably a rare, Nearctic member of the Great Lakes fauna.

C. Crustaceans

The introduced Crustacea of the Great Lakes (Table 5) are not as well studied as the mollusks. Studies of the zooplankton of the Lakes did not begin until the late 1800s (Balcer et al. 1984) after potential mechanisms for their dispersal into the Lakes had been present for decades. For this reason, several species considered native to the Lakes that have discontinuous or "holarctic" distributions could in fact be introduced.

Order: Cladocera

Cercopagidae:

Bythotrephes cederstroemi SPINY WATER FLEA OR BC

Bythotrephes cederstroemi, a European predatory cladoceran, was first observed in North America in Lake Huron in December, 1984 (Bur et al. 1986). It was soon found in Lake Erie in 1985 (Bur et al. 1986), Lake Ontario in 1985 (Lange and Cap 1986), Lake Michigan in 1986 (Evans 1988), and Lake Superior in 1987 (Cullis and Johnson 1988). The cladoceran is thought to have entered the Great Lakes in the ballast water of European ocean going vessels in the late 1970s or early 1980s (Sprules et al. 1990). BC's rapid dispersal throughout the Lakes probably involved ballast transfer within the Lakes in Great Lakes vessels (lakers) and/or separate introductions at different locations directly from Europe (Sprules et al. 1990). Sprules et al. (1990) speculated that BC could have originated from the port of Leningrad because of the large amount of ship traffic carrying grain from Great Lakes ports to Leningrad in the late 1970s and early 1980s and the abundance of BC in this freshwater port.

Bosminidae:

Eubosmina coregoni WATER FLEA

The first Great Lakes record of this European cladoceran was in Lake Michigan in 1966 (Wells 1970). Davis (1968) and Wells (1970) identified it as a form of the variable native species

Bosmina coregoni. In their revision of the genus *Eubosmina*, Deevey and Deevey (1971) noted that the major differentiating characteristic of the European species *Eubosmina coregoni* from other species of *Eubosmina* and *Bosmina,* is the lack of a mucro or tail spine, a characteristic of Davis and Well's specimens, thus identifying the North American populations correctly. Deevey and Deevey (1971) mention the possibility of *E. coregoni* being an introduction from Europe, but give it a holarctic distribution because of its widespread abundance. By 1968, it had also been identified in Sanctuary Lake (Pymatuning Reservoir), Pennsylvania, Lake Huron, Lake Ontario, and Lake Erie (Davis 1968, Deevey and Deevey 1971). Since these early records, *Eubosmina coregoni* has spread into all the Great Lakes and become one of the dominant zooplankters (Leach 1973, Czaika 1974, Patalas 1975 and Evans 1988). *Eubosmina coregoni* was most likely introduced into the Great Lakes in ballast water and, similar to *Bythotrephes*, was transferred from lake to lake by Great Lakes vessels.

Subclass: Copepoda

Suborder: Calanoida

Temoridae:

Eurytemora affinis CALANOID COPEPOD

The occurrence of this copepod in Lake Erie in 1961 was first reported by Engel (1962). Earlier studies in 1958 in Lake Ontario had recognized a copepod of the genus *Eurytemora* that was not identified to species but was most likely *Eurytemora affinis* (Anderson and Clayton 1959, Faber and Jermolajev 1966). By 1972 it had spread into Lake Michigan (Robertson 1966), Lake Huron (Faber and Jermolajev 1966), and Lake Superior (Patalas 1972). Native to salt, brackish, and fresh waters, it is more abundant in bays and harbors of the Great Lakes than in the open Lakes (Balcer et al. 1984) which could facilitate dispersal among the Lakes in the ballast water of ships. *Eurytemora* was most likely introduced from the North American Atlantic Coast (or from the western European coast) in the ballast water of ships coming through the St. Lawrence or Erie

Canal systems (Faber and Jermolajev 1966).

Diaptomidae:

Skistodiaptomus pallidus CALANOID COPEPOD

Skistodiaptomus pallidus was first observed in Lake Ontario in 1967 (Patalas 1969). Since then, it has been reported in low numbers from Lakes Ontario, Erie and St. Clair (Leach 1973, Czaika 1974 and 1978, and Cap 1979). Wilson and Yeatman (1958) reported that *Skistodiaptomus pallidus* is found in ponds and lakes ranging from north central and plains states south to Texas and Louisiana; Pennak (1978) notes that it is distributed in the Mississippi drainage. Thus, the natural distribution of this copepod may include the outlying parts of the Great Lakes watershed. Citing the records obtained since 1969, Robertson and Gannon (1981) report it as a small lake form that "occasionally" enters the Great Lakes. *Skistodiaptomus pallidus* could have easily been introduced into the Great Lakes watershed with the equipment or bait of fishermen and recreational boaters or with fish introduced from hatcheries in the Mississippi drainage.

Order: Amphipoda

Suborder: Gammaridea

Gammaridae:

Gammarus fasciatus GAMMARID AMPHIPOD

This common freshwater gammarid represents a possible introduction into the Great Lakes from the Hudson, Delaware, or Chesapeake drainage systems. Early records (Hubricht and Mackin 1940) suggest a striking disjunct distribution of Lake Michigan populations from the main Atlantic drainage populations. Chase et al. (1959) noted the disjunct distribution and suggested that it was "probably introduced" into the Great Lakes. Bousfield (1958) however, recorded a more widespread distribution in the freshwater drainages of the Great Lakes and the St. Lawrence, Hudson, Delaware, and Chesapeake Rivers. While early studies doubtless undersampled these drainage systems, it remains possible that the current distribution of this amphipod is due to the range of human activities that could have altered its natural distribution, including releases with ballast water, aquatic plants, stocked fish and fish bait. As of 1940, the extent of the ranges of freshwater amphipods was not well studied (Hubricht and Mackin 1940), and, consequently, the natural distribution of *Gammarus fasciatus* cannot be determined. While Weckel (1907) recorded *Gammarus fasciatus* from the Great Lakes and the Mississippi River systems, the natural distribution is further complicated by Hubricht and Mackin's (1940) suggestion (based upon her illustrations and locations) that Weckel's material also contained *Gammarus limnaeus*. A benthic organism, *Gammarus fasciatus* could have easily been introduced in solid ballast or ballast water of ships plying the St. Lawrence or Erie Canal systems.

D. Oligochaetes

Few studies have focused on the North American oligochaete fauna (Pennak 1989) and, as a result, the distributions of native and introduced species are largely unknown. Some species previously thought to be introduced now have distributions that are considered holarctic; conversely, some so-called "holarctic" species may in fact be introduced. Taxonomic problems are also associated with the oligochaetes, leading to further uncertainty on the status of native and introduced species (Table 6).

Mechanisms for oligochaete introductions have occurred since the earliest settlers arrived in North America. Oligochaetes often form a cocoon when undergoing sexual reproduction which will commonly attach to rocks, plants, and solid debris (Stephenson 1930). These materials were commonly used as ship's ballast in the early maritime history of the Lakes. After the settlement of the Great Lakes basin, aquatic plants for use in aquaria and ornamental ponds were often imported, also providing a means for oligochaetes to enter the Lakes.

Lumbriculidae:

Stylodrilus heringianus

Stylodrilus heringianus was first collected in the Great Lakes watershed in 1962 in the North Channel and in the St. Mary's River near Sugar Island, Michigan (Brinkhurst 1966). Brinkhurst (1966) also noted records from Amherst, Massachusetts in 1960, from Lake Michigan, south of Holland, in 1964, and undated specimens from Lake Huron and New Brunswick, Canada. Because of the discovery of specimens across Canada from British Columbia to Newfoundland, because populations were found in localities with "no historical connection" to each other, and because most lumbriculids are believed to be naturally holarctic, the status of this species as an introduction from Europe is now questionable (Brinkhurst 1978, 1986). Brinkhurst (1986) noted that the aquarium trade and shipping may have introduced this species, but because of the lack of concrete historical records its biogeographic history may never be known. The species' capability of transoceanic synanthropic dispersal is indicated, however, by its introduction to New Zealand

(Brinkurst 1986). It is now extremely abundant in the Great Lakes (Cook 1975, Loveridge and Cook 1976, Barton and Griffiths 1984 and Brinkhurst et al. 1968).

Naidae:

Ripistes parasita

The first occurrence of this easily identified species (Brinkhurst 1986) in North America was in 1978 in several New York State rivers and in the New York canal system (Simpson and Abele 1984). These records, located outside of the Great Lakes watershed (e.g. Chemung River near Corning, Chenango River near Binghamton, Cohocton River near Campbell, and in the Mohawk River Barge Canal), were obtained from artificial substrates used in biological monitoring studies (Simpson and Abele 1984). Barton and Griffiths (1984) obtained the first Great Lakes specimens from two sites in the North Channel in 1980. Records of the oligochaete for Southern Lake Superior at Preque Isle Point, Michigan (Klemm 1985) give it a fairly wide distribution in North America. *Ripistes parasita* naturally occurs in the European (Klemm 1985) palearctic region (Simpson and Abele 1984) and the Great Lakes records are the first outside of its natural distribution. Despite the chronology of these records in the Great Lakes basin, the worm probably was introduced into the Great Lakes in ballast water and later spread into the inland canals and rivers.

Tubificidae:

Branchiura sowerbyi

Branchiura sowerbyi, a native of Asian tropical and subtropical areas (China, Burma, India and Japan) has been widely introduced into Europe, North America and Africa (Brinkhurst 1965, Aston 1968). It was originally described from aquaria containing tropical plants imported from Asia at the Botanical Gardens in Kew, England (Beddard 1892, Mann 1958). Once described, it was quickly observed in many other localities in Europe that contained Asian imported plants (hothouses, ornamental ponds and botanical gardens) and in heated effluents in natural bodies of water (Brinkhurst 1965). In 1930, the worm was discovered in Buckeye Lake, Ohio (Spencer 1931). Since this first record, it has been widely introduced throughout North America, most likely with aquatic plants or through the aquarium trade. The first Great Lakes record was from 1951 in the Kalamazoo River in Comstock, Michigan and later in Western Lake Erie and Lake St. Clair in 1963 (Brinkhurst 1965). In 1963 studies in Sandusky Bay, Lake Erie, the worm was the most abundant oligochaete present (Wolfert and Hiltunen 1968).

Phallodrilus aquaedulcis OLIGOCHAETE

Phalladrilus aquedulcis a European oligochaete previously known only from the River Weser in Germany and inland caves in Spain and France, was first observed in the Niagara River in 1983. This established population is the first record for the species in North America (Farara and Erseus 1991). The oligochaete was probably introduced into the Great Lakes in the ballast water of ships plying from the River Weser region in Germany.

Potamothrix

The status of the European genus *Potamothrix* in North America has changed several times since studies first began reporting species of *Potamothrix* in Great Lakes drainages in 1952. At first, they were thought to have been introduced into the Lakes, but later, as in the case of *Stylodrilus heringianus*, when more widespread distribution records were discovered, several of the species were given holarctic status.

Potamothrix bedoti

Timm (1972) states that *Potamothrix bedoti* is "obviously" introduced into North America. The earliest known collections of this species in the Great Lakes are difficult to determine because it was considered a variant of *Potamothrix bavaricus* until more recent studies (Spencer 1978a and

Timm 1972) regarded them as separate species. The first records of *Potamothrix bavaricus* in the Great Lakes basin are reported by Brinkhurst (1965) from Cayuga Lake in 1918. *Potamothrix bedoti* is known from palearctic areas and in North America, it is limited to the Great Lakes basin (Spencer 1978a, Klemm 1985, Brinkhurst 1986).

Potamothrix vejdovskyi

The earliest collection of *Potamothrix vejdovskyi* in the Great Lakes is from Lake Erie in 1963 (Brinkhurst et al. 1968). Other collections have been reported from Lake Huron, Lake Michigan, Lake Erie, the North Channel and St. Mary's River (Brinkhurst 1966). Before these Great Lakes records, the only collections of this oligochaete were from the Soviet Union on the Danube and the Lower Dnieper Rivers. Since these initial records, the worm has been collected at sites outside of the Great Lakes drainage in Virginia and Ohio (Brinkhurst 1986), perhaps leading Klemm (1985) to give it a holarctic distribution.

Psammoryctides barbatus

Psammoryctides barbatus is a European oligochaete that was first observed in North America in the lower St. Lawrence River by Vincent (1979). Although this location in the St. Lawrence River is outside the geographic range of this analysis, its spread into the Great Lakes is possible. *Psammoryctides barbatus* is unmistakably an introduced European species (Brinkhurst 1986) brought to the St. Lawrence River through international shipping activities.

Spirosperma ferox

The occurrence of this worm in North America was first reported by Brinkhurst (1966). Previously known to be abundant in palearctic areas and Iceland, the first Great Lakes collections are from 1962 in Lake Ontario (Brinkhurst 1966). By 1966, the worm was also identified in Lakes Huron, Erie and Superior (Brinkhurst 1966). Because the worm occurs in Iceland, Brinkhurst (1966) suggests that it may be holarctic. He considered it introduced because there were no North American records until the early 1960s and (as of 1966) the North American distribution was limited to the Great Lakes and Pennsylvania. The oligochaete now is considered holarctic with a "patchy" distribution encompassing eastern North America, the Great Lakes and Louisiana (Klemm 1985).

Oligochaetes previously thought to be introduced

Pristina acuminata

Spencer (1978b) recorded the first and only observation of this Asian oligochaete in North America from Lake Erie (Brinkhurst 1986). After first being described by Liang (1958) from China, the oligochaete's distribution was not augmented by new records until Spencer's (1978b) collections. Minor differences that occurred between Liang's and Spencer's descriptions were attributed to the geographic distance separating the two populations (Spencer 1978b). The North American specimens were considered a nearctic population of the species (Spencer 1978b). Since the Chinese materials cannot be obtained for analysis, doubt has been raised about the identity of Spencer's specimens (Brinkhurst 1986). The North American records of *Pristina acuminata* may be the result of a chance unsuccessful introduction or a misidentification.

Potamothrix hammoniensis

Questionable records noted by Klemm (1985) from Green Bay, Lake Michigan and Ontario, Canada, were never validated (Brinkhurst 1986). Great Lakes records for this species probably represent *Potamothrix vejdovskyi* (Brinkhurst 1986).

Potamothrix moldaviensis

The first collections of *Potamothrix moldaviensis* were made in the St. Lawrence River at Prescott, Ontario in 1952 (Brinkhurst 1965). It was quickly found in Lakes Erie, Huron and Michigan (Brinkhurst 1966) and eventually identified in all the Great Lakes (Brinkhurst 1976).

The most recent treatments (Klemm 1985 and Brinkhurst 1986) give it a holarctic distribution.

Ryacodrilus punctatus

This oligochaete was first reported in North America in 1973 in Lake Superior (Cook 1975). The only other occurrence of *Ryacodrilus punctatus* in the world is from Ohrid Lake (Brinkhurst 1978), which straddles the Albanian/Yugoslavian border. Brinkhurst (1986) is skeptical about the identity of the North American specimens.

E. Disease pathogens

Only two fish diseases are known to have been introduced into the Great Lakes, one bacterium and one protozoan (Table 7). These diseases were introduced with imported fish into aquaculture facilities. The number of disease pathogens introduced into the Great Lakes (2) is relatively low compared to the number of native fish diseases (374 in Canada) (Dobson and May 1984).

Bacteria:

Aeromonas salmonicida FURUNCULOSIS

Aeromonas salmonicida is a gram-negative bacterium that causes furunculosis, trout and goldfish ulcer disease, carp erythrodermatitis and other infections in species of warmwater and marine fish (Bullock et al. 1983). First discovered as the disease agent of salmonid furunculosis in Germany, *Aeromonas salmonicida* was introduced into the Great Lakes in 1937 when it was imported with brown trout from the west coast (R. Horner, Illinois Dept. of Cons., personal communication 1990). Although effective control measures using antimicrobial drugs are known to treat trout ulcer disease, these procedures are not as successful for the other diseases that the pathogen causes (Bullock et al. 1983).

Protozoa:

Myxosoma cerebralis SALMONID WHIRLING DISEASE

Salmonid whirling disease, caused by the protozoan myxosporean *Myxosoma cerebralis*, is a disease that causes abnormalities in the skeletal structure and pigmentation of salmonids (Wolf and Markiw 1985). The protozoan infects and damages the cartilage of the fish causing abnormal skeletal structure, which induces the tale-chasing swimming behavior for which the disease was named (Wolf and Markiw 1985). A black discoloration of the tail of the fish or "blacktail" is also a sign of the disease (Wolf and Markiw 1985). The protozoan spends part of its life cycle in the oligochaete *Tubifex tubifex*. Although thought to have arrived in the 1950s, the disease was first observed in the Great Lakes drainage in 1968 in Ohio at a private aquaculture facility (Anonymous 1988). The disease is mostly known from hatcheries and has not been seen extensively in the wild (Wolf and Markiw 1985). Fish hatcheries have found that the protozoan can be controled by using concrete in their facilities to reduce inhabitation by *Tubifex tubifex* (Anonymous 1988).

F. Other invertebrates

Several other freshwater invertebrates have been introduced into the Great Lakes (Table 8). These include a flatworm, two bryozoans and a freshwater jellyfish. Although introduced aquatic insects in the Great Lakes (i.e. *Acentropus niveus* (Forbes 1938, Judd 1950) and *Tanyphyrus lemnae* (Bayer and Brockmann 1975 and Pennak 1978)) and in North America (i.e. *Phytobuis valatus* (Pennak 1978) and *Dryops viennensis* (Brown 1972)) are known, a comprehensive study of this group would be beyond the scope of this study. The distributional history and taxonomy of the aquatic insects of the Great Lakes is not known well enough to determine which species have been introduced.

Platyhelminthes:

Dugesia polychroa FLATWORM

Ball (1969) first reported this Palearctic European flatworm in North America. The worm has been found in the St. Lawrence River, Lake Champlain and Lake Ontario in 1968 (Ball 1969). The Richelieu River, a navigable river, connects the St. Lawrence River and Lake Champlain (Ball 1969), thus, all the areas where this worm has been found are connected by navigable waterways. Kenk (1974) in his treatment of the triclads of the world, noted the species as introduced into the St. Lawrence River system. The worm was probably introduced in the ballast water of ships (Ball 1969).

Bryozoa:

Lophopodella carteri BRYOZOAN

Rogick (1934) reported the first records of this bryozoan in North America in Western Lake Erie's Island region in 1933. Rogick noted that American specimens were very similar to others collected in Indian material and notes the possibility that the species may have been observed in the United States earlier but identified incorrectly. The bryozoan is widespread in Asia and is known from sporadic collections from Africa and Australia (Wood 1989). In North America, this disjunct, sporadic distribution (Wood 1989) provides evidence that the species is introduced.

Plumatella casmiana BRYOZOAN

Rogick (1941) first reported this Eurasian bryozoan in North America from Western Lake Erie's Island region in 1932. Previously the species had been recorded only from Japan, U.S.S.R., and West Java (Rogick 1941). Pennak (1989) reported the species from Lake Erie, Indiana, Michigan and Colorado. Wood (1989), however, notes that the species, "nearly cosmopolitan" is known from all continents except Australia. Whether this distribution reflects the natural dispersal of the species or potentially introduced populations is unknown and it will not be considered introduced into the Great Lakes because of this uncertainty.

The bryozoan life cycle includes a larval stage that swims freely for several minutes to 24 hours and a dormant stage of statoblasts that are resistant to adverse environmental conditions (Pennak 1989). Viable colonies of *Lophopodella* have been known to arise from statoblasts that had been desiccated for over four years (Pennak 1989). *Plumatella* statoblasts are not as resistant, but still can form colonies after two years of desiccation. Bryoza could be transported with aquatic plants, ship's solid ballast or ballast water, or released from aquaria.

Hydrozoa:

Cordylophora lacustris HYDROID

This hydrozoan was first observed in Chagrin Harbor, Ohio in Lake Erie in 1956 (Davis 1957). *Cordylophora lacustris* is a widespread euryhaline species known from locations in Europe, Australia and Africa and the western Atlantic Coast (Davis 1957). Hubschman and Kishler (1972) reported established populations of this hydroid in western Lake Erie.

Craspedacusta sowerbyi FRESHWATER JELLYFISH

Craspedacusta sowerbyi, an Asian freshwater jellyfish (Kramp 1950) was first observed in the United States in 1916 near Frankfort, Kentucky in Benson Creek (Garman 1916). The first collections in the Great Lakes were in 1933 in the Huron River near Ann Arbor, Michigan (Woodhead 1933) and in 1934 in Lackawanna, New York "a few hundred feet" from Lake Erie (Robertson 1934). Other Great Lakes collections have been from Lake Erie (Hubschman and Kishler 1972) and inland Michigan lakes where it reaches its northernmost distribution (Bushnell and Porter 1967, Smrchek 1970) The organism is often found in artificial bodies of water like ponds and quarries throughout the United States but is not limited to these habitats (Garman 1916, Brooks 1932, Schmitt 1939, Dexter et al. 1949, Lytle 1960 and Bushnell and Porter 1967). The sporadic nature of this jellyfish's distribution and its preference for artificial habitats indicate that it could possibly be an aquarium release or a release with aquatic plants (Bushnell and Porter 1967).

G. Plants

Botanists have observed the presence of exotic plant species in the Great Lakes since the 1840s. Although many later invasions have been well documented through the examination of herbarium specimens (Stuckey 1966 and1980), the invasions occurring early in the settlement of the Great Lakes region, like bittersweet nightshade, were not documented and the details of their introduction into the Lakes remain unknown. The large group of plants (Table 9) discussed below include any introduced plant that is associated with water, ranging from submerged plants to trees that commonly grow on shorelines.

Marsileaceae:

Marsilea quadrifolia EUROPEAN WATER FERN

European water fern was first introduced into North America in Bantam Lake in Litchfield, Connecticut (Gray 1867). From this population, the plant was introduced into other parts of the eastern United States (Britton and Brown 1913). In the Great Lakes basin, the plant has been found in Cayuga Lake in New York State and in Haldimand County, Ontario. Wiegand and Eames (1925) reported the plant from the shores of Cayuga Lake and several other sites within the Cayuga Lake basin. They noted that the plant was introduced by early botanists of the area. The earliest flora of the Cayuga Lake area, however, did not include the Pteridophyta (Dudley 1886) so the details of the introduction, which most likely occurred before 1900, are unknown. Montgomery (1956) reported an established population of *Marsilea quadrifolia* from Nanticoke in Haldimand County, Ontario in 1951. Nanticoke is near the north shore of Lake Erie east of Port Dover, Ontario. Fernald (1950) noted that this plant spreads rapidly once it has become established.

Typhaceae:

Typha angustifolia NARROW LEAVED CATTAIL

The distributional history of the narrow leaved cattail, a brackish water species native to the Atlantic Coast is debatable. The plant is thought to have invaded inland slowly with the early canal, railroad, and highway systems. It began a rapid expansion inland through central New York into the Great Lakes Basin in the first half of the 20th century when the de-icing of highways using salt became more widespread. The status of the plant in the eastern part of the Lake Ontario watershed is uncertain. Early New York floras (Torrey 1843, Dudley 1886) do not limit the range of the species to coastal areas but do indicate that the plant is less frequent further west into the Great Lakes drainage basin (Day 1882, Britton and Brown 1913). Whether these inland records represent early introduced populations or the inland extent of the cattail's range is unknown. The plant, however, has invaded the Great Lakes as far as inland as Michigan's upper peninsula (Voss 1972).

Sparganiaceae:

Sparganium glomeratum BUR REED

The first occurrence of the European bur reed in North America is from Lake Itasca, Minnesota in 1893 (Lakela 1941). This introduction was not successful, however, and the plant was not collected again in North America until 1927 when an apparently established population was discovered in Saguenay County, Quebec in the Natashaquan River region (Lewis 1931). Lakela (1941) later found a population of the plant in Duluth, Minnesota in a bog near Superior Bay. These are the only two locations known for this plant in North America (Fassett 1957, Hotchkiss 1972). Gleason (1950) considers this species circumboreal, but Fassett (1957) notes its European distribution and the Duluth, Minnesota Lake Superior record. The mechanism through which it was introduced remains unknown.

Zosteraceae:

Potamogeton crispus CURLY PONDWEED

Stuckey (1979) reviews the introduction and spread of this common European aquatic plant. Although reports of the species date back to 1807, the earliest verifiable records of the plant in North America are from the 1860s in Wilmington, Delaware and Lancaster, Pennsylvania. In the 1880s, the plant was found in Arlington, Massachusetts and Keuka Lake, New York. The Keuka Lake record, from 1879, is the first Great Lakes basin record for the species. By 1884 *Potamogeton crispus* was reported throughout central New York and near Niagara Falls. It is currently very common throughout the Great Lakes basin. It is more abundant in Lakes Ontario, Erie and Michigan than in Lakes Superior and Huron, where it continues to spread. *Potamogeton crispus* is known to have been introduced into parts of the Great Lakes basin deliberately as food for waterfowl and has been associated with fish hatcheries, indicating potential transport between basins associated with fish stocking activities (Stuckey 1979).

Najadaceae:

Najas marina SPINY NAIAD

Spiny naiad, a plant preferring brackish and alkaline waters was first found in North America in 1864 in central New York's Onondaga Lake near Salina, New York (Stuckey 1985). The population was growing near a salt mine in brackish water. Fossil records of this plant from the midwest indicate that it was present in North America prior to glaciation supporting debate about whether the newly discovered populations were indigenous or non-native. Two interpretations of the plant's distribution in the Great Lakes have been outlined by Stuckey (1985). He theorizes that the plant was pushed south during glaciation and reinvaded glacial lakes when the ice receded. He suggests that the species persisted in areas where the habitat remained favorable and reinvaded some areas, such as the western Great Lakes region, more recently. The introduction of the plant from Europe into habitats made brackish and alkaline by human activities (such as areas around salt mines) is also possible. Central New York was a very active botanical center in 1864 and the possibility that the plant was overlooked for years is not likely. We consider the introduction of spiny naiad from Europe into the industrialized area around Onondaga Lake to be a more likely scenario than the persistence of preglacial populations.

Najas minor MINOR NAIAD

This European native was observed in North America in 1934 in the Hudson River near Troy, New York (Clausen 1936). The plant was clearly established in this location in "great beds" in shallow water (Clausen 1936). In the same year, Muenscher and Clausen found populations of the plant growing in several different areas in and near the Hudson River (Clausen 1936). The plant was soon introduced into the Great Lakes drainage in Ithaca, New York by W.C. Muenscher, who wanted to see if it would persist in Cayuga Lake, in 1935 (Clausen 1936). After these original introductions, the plant rapidly spread into the Great Lakes system. It was identified in Monroe County, New York in 1939 (Merilainen 1968) and in Pte. Moullee State Game Area in Michigan in 1949 (Voss 1972).

Butomaceae:

Butomus umbellatus FLOWERING RUSH

This European marsh species was observed in North America in La Prairie, Quebec, a town across the St. Lawrence River from Montreal, in 1897 and first collected there in 1905 (Core 1941). The plant quickly spread and became established along a large part of the St. Lawrence River (Core 1941). In 1930, collections of the plant were made in the vicinity of the town of River Rouge, south of Detroit, Michigan along the Detroit River (Farwell 1938). The over 500 mile disjunction in distribution from the nearest population in Quebec to the population in Michigan indicates that the Michigan population was introduced either from the La Prairie population or directly from Europe (Stuckey 1968). The introduction into Detroit must have occurred earlier than the 1930 collections suggest because Farwell knew of observations of a large population of the plant in the River Rougue area before 1918. These populations were diminished when Ford Motor

Company apparently reclaimed the marshland where these immense stands of flowering rush had occurred (Farwell 1938). The introduction of *Butomus umbellatus* with shipping activities into Montreal and Detroit is likely. The population of flowering rush at the River Rouge site is thought to either have been directly introduced from Europe or introduced from the St. Lawrence River (Stuckey 1968). Other theories concerning the introduction of flowering rush into North America date it much earlier. Farwell (1938) suggested that the introduction could have occurred as early as the mid 1600s. Stuckey (1968) however, noted that the rate that the populations have spread after their initial discovery indicated that they did not arrive much earlier than their discovery.

Hydrocharitaceae:

Hydrocharis morsus-ranae EUROPEAN FROG-BIT

Hydrocharis morsus-ranae was imported into the Central Experimental Farm in Ottawa, Canada from Zurich, Switzerland in 1932 (Minshall 1940, Roberts et al. 1981). The species was planted in a trench connecting an arboretum pond to the Rideau Canal, but it was not observed until 1936 when it had invaded the pond (Minshall 1940). By 1953 the frogbit had gradually spread into the Rideau Canal, its connecting waters, and the Ottawa River and by 1958 it was well established in the St. Lawrence River near Montreal (Dore 1954, 1968). In 1976, *Hydrocharis morsus-ranae* was found in the Bay of Quinte, Lake Ontario and in 1976 it was discovered in Rondeau Park on the north shore of Lake Erie (Catling and Dore 1982). Lumsden and McLachlin (1988) note the plant's continued spread into western Lake Ontario marshes. The plant will likely spread further into the Great Lakes drainage.

Gramineae:

Echinochloa crusgalli BARNYARD GRASS

Barnyard grass, a European native, is noted in some of the earliest American floras (Michaux 1803, Nuttall 1818, Torrey 1824). Because it arrived before the flora of the Great Lakes was well studied, records of its introduction do not exist, although it is thought to have arrived in colonial times. Because the plant is commonly found around barnyards (Fassett 1957) it is possible that it was imported with animals in bedding or feed. The plant is now considered "nearly cosmopolitan" (Fernald 1950). Although *Echinochloa crusgalli* has a close North American relative, *Echinochloa pungans*, the species are distinct and early identifications were likely correct (Fassett 1949).

Glyceria maxima REED SWEET-GRASS

The first records of this European species in North America were from a Lake Ontario marsh between Hamilton and Dundas, Ontario in 1940 (Dore 1947). From the 1940 collections until 1946, *Glyceria maxima* was discovered from three additional sites in Ontario (Dore 1947). These firmly established populations had probably been present for years before they were first observed (Dore 1947). The grass, a favorable and economical forage species for marshy land, is thought to have been introduced early through cultivation or as discarded packaging material for crockery imported by settlers (Dore 1953). The oldest stands of the plant seem to be concentrated in areas of "Old Ontario" and other early settlements (Dore 1953).

Poa trivialis ROUGH-STALKED MEADOW GRASS

Naturalized from Europe by the early 1800s (Nuttall 1818), *Poa trivialis* is a grass species commonly used for hay or pasturage (Torrey 1843). Dudley (1886) reported the plant from marshes, fields and deep swamps in the Cayuga Lake basin in central New York and considered it indigenous. Although the details of this plant's introduction into North America are unknown, it could have been introduced early as a forage species for livestock or imported with the livestock as feed or bedding. The grass is known from throughout the Great Lakes basin in moist fields, moist woods and marshes (Wiegand and Eames 1925, Zenkert 1934, Montgomery 1956 and Voss 1972). More recently, it may have been transported and introduced with lawn seed (Swink and Wilhelm 1979).

Puccinella distans WEEPING ALKALI GRASS

Gray (1867) first reported weeping alkali grass in North America from coastal salt marshes and later Gray (1889) noted that it was also found on ballast. The species was not reported in the Great Lakes basin until Wiegand and Eames (1925) found the Eurasian and North African grass from brackish meadows in Montezuma and Syracuse, New York. In Ontario, the plant was found in railroad yards and at Rainy River in the Lake Superior drainage (Montgomery 1956) and in southern Ontario in alkaline and calcareous areas (Catling and McKay 1980). More recent records from the Great Lakes indicate that the plant is common on saline highway margins and other salty ground (Voss 1972, Swink and Wilhelm 1979).

Cyperaceae:

Carex acutiformis SWAMP SEDGE

This European marsh plant is known from St. Joseph County, Michigan where it was first observed on the shores of St. Joseph Lake at Notre Dame in 1951 (Swink and Wilhelm 1979). In 1976, the population persisted (Swink and Wilhelm 1979). The means through which the plant was introduced remains unknown.

Carex disticha SEDGE

The first North American records for *C. disticha*, a Eurasian sedge, are from Belleville, Ontario in 1866 (Fernald 1942). Although it was originally thought to be native at this site, Catling et al. (1988) noted that the population is probably nonindigenous. Since this early record, the plant has been recorded from several locations, including Iles de Boucherville near Montreal, Quebec in 1927, 1929 and 1940 and at Collingwood in Simcoe County, Ontario in 1972 (Catling et al. 1988, Fernald 1942). The plant is a dominant forage crop in parts of the USSR (Catling et al. 1988). Its use for hay and straw indicates possible introduction with animal forage and bedding or in packaging materials.

Carex flacca SEDGE

Fernald (1950) noted *Carex flacca* from "dry fields and roadsides" from Nova Scotia, Quebec, Ontario, and Michigan. Voss (1972) reported early collections of this European plant by Farwell in the Detroit River on Belle Isle in 1896 and 1903. Currently, the plant is known from Lake Huron's calcareous meadows (A. Reznicek, University of Michigan, personal communication, 1990). Since Fernald (1950) is a more general treatment, we will consider the plant a Great Lakes marsh species based on Voss (1972) and Reznicek's observations. *Carex flacca* was probably introduced into the Great Lakes in the solid ballast of ships, in animal bedding or packaging materials.

Juncaceae:

Juncus compressus FLATTENED RUSH

Stuckey (1981) reviewed the introduction of the Eurasian flattened rush into North America. Although Bartlett (1906) first reported its presence in North America from 1904 collections, *Juncus compressus* was misidentified as *Juncus gerardi* prior to 1904 (Stuckey 1980). According to Stuckey, Marie-Victorin (1929) believed that *Juncus compressus* was brought to North America in forage used to feed military horses. A species favoring brackish, calcareous habitat, its introduction into locations in the interior often can be associated with commerce and disturbed man-made areas. For example, prior to 1895, the rush was observed in Cayuga Lake at a glass factory which was near a salt works (Wiegand and Eames 1925). Wiegand and Eames (1925) believed the plant had been brought to the lake with the sand used in manufacturing the glass. The plant is also known from the Toronto, Ontario area.

Juncus gerardi BLACK-GRASS RUSH

Black grass rush, a dominant salt marsh species, is found on the Atlantic and Pacific Coasts (Muenscher 1944, Stuckey 1980, Zenkert 1934). The earliest known Great Lakes records of the plant are from saline marshes in Salina, New York in 1864 and near Chicago in 1862 (Stuckey 1980). Because its occurrence inland is associated with man-made, often saline, habitats, it is probable that the introduction of the plant was aided by commerce. The occurrence of the rush on ballast grounds and its use as packaging material support this argument. The plant is known from Lakes Ontario, Erie, Huron and Michigan (Stuckey 1980).

Juncus inflexus RUSH

Fernald (1950) noted this plant from New York to Michigan. Voss (1972) noted the first records of this European species in Michigan in 1936 near Hancock, Michigan. Because Britton and Brown (1913) did not include this plant in their North American flora, it probably was introduced sometime in the early 20th century. The means through which this plant was introduced remains unknown.

Iridaceae:

Iris pseudocorus YELLOW FLAG

Iris pseudocorus, the yellow flag, a popular ornamental garden flower until other varieties gained favor, often escaped from cultivation to form established stands in marshes, shores and other wet areas (Cody 1961, Dudley 1886, Judd 1953, and Voss 1972). Dudley (1886) first reported the plant from a swamp near Ithaca, New York. This record, along with a report of a Massachusetts population, were the first recorded escapes of yellow flag from cultivation (Gray 1889). Cody (1961) reviews the Canadian records of the *Iris pseudocorus*, which was first observed in Ontario in 1940.

Salicaceae:

Salix spp. WILLOWS

Known to escape from cultivation by the early to mid 1800s (Nuttall 1818, Gray 1848), three species of willows have been widely introduced into North America (Fernald 1950). The trees were imported for various purposes. *Salix alba*, white willow and *Salix fragilis*, crack willow are ornamental introductions that are known to have regularly escaped from cultivation. *Salix purpurea*, purple willow, is cultivated for ornamental purposes and used in basket weaving (Fernald 1950). The trees prefer river and stream banks and lake shores (Dudley 1886, Zenkert 1934, Voss 1985). The branches of *Salix fragilis* often break and root in favorable habitat (Deam 1940) and each of the trees will hybridize with other willow species forming several varieties (Fernald 1950, Voss 1985).

Betulaceae:

Alnus glutinosa BLACK ALDER

This Eurasian species has been widely introduced as an ornamental tree and commonly escapes to river banks and lake shores (Voss 1985). Wiegand and Eames (1925) discussed how the tree clones by spreading through its roots on river banks and along lakeshores. The earliest known records of this species escaping from cultivation are from the late 19th century, when it was reported from "Newfoundland to New Jersey and Illinois (Britton and Brown 1913)." It was not noted in Gray (1889).

Myricaceae:

Myriophyllum spicatum EURASIAN WATER MILFOIL

Although the plant is thought to have arrived much earlier, the first validated occurrence of Eurasian watermilfoil, a common aquarium species, in North America is from 1881 in the Potomac River, Virginia (Reed 1977). The plant, although present in North America from the 1880s onward, did not cause any problems until the late 1950s when, due to increases in the calcium concentrations in Chesapeake Bay, the populations grew to problematic proportions. For years, the taxonomy of the North American watermilfoil was under debate, and, in most cases, all species of *Myriophyllum* were referred to as *Myriophyllum exalbescens*. Reed (1977) reviewed the taxonomic difficulties and documented the arrival and spread of the plant in the United States in more detail. In the Great Lakes basin, the first record occurred in 1882 in Paddy's Lake near Oswego, New York. No specimens, however, were collected again until 1960 when the plant was found at Sodus Bay, Lake Ontario and in Rochester, New York. Many new collections were made in New York and in other Great Lakes states in the years immediately following these first records. Eurasian watermilfoil was found in Michigan in 1965 (Coffey and McNabb 1974) and in the St. Clair-Detroit River system in the 1960s (Schloesser and Manny 1984). Although the plant has not yet become a major problem in the Great Lakes, the abundance of Eurasian water milfoil in the waters of the watershed has caused many problems. The extensive beds of the plant have created problems in recreational use of the water and have competed with native aquatic plants. Such methods as cutting and harvesting, water drawdown and herbicides, have been used to control the plant (Coffey and McNabb 1974). The plant most likely entered the Great Lakes basin through aquarium release and transport associated with shipping traffic.

Polygonaceae:

Rumex longifolius DOCK

Voss (1985) noted that *Rumex longifolius* and *Rumex domesticus* are synonymous and reported records of the Eurasian plant from Isle Royle from 1901-1960. The 1901 date is the earliest validated date available even though an earlier record may exist, since some of the collections reported in Gray's 7th edition of *Rumex patientia* were actually *Rumex longifolius* (Fernald 1950). Britton and Brown (1913) reported *Rumex patientia* from various localities on the east coast and in the mid-west. Gray (1889) noted *Rumex patientia* from New England and New York.

Cruciferae:

Nasturnum microphyllum WATER CRESS

Nasturnum officinale

The importation of water cress and its escape from cultivation was so widespread in the early-to-mid 1800s that its naturalization was not well documented. Established populations, most likely rising from plants cultivated for culinary purposes, were first observed in North America near Niagara Falls, Canada in 1847 (Gray 1848). At this time, however, water cress was probably established in many areas of the Great Lakes watershed. Voss (1985) cited records from Ann Arbor, Michigan from 1857. Since these early records, water cress has become established throughout North America (Voss 1985).

Rorippa sylvestris CREEPING YELLOW CRESS

This European native was first reported in North America from Philadelphia in 1818 (Stuckey 1966). The first observations of creeping yellow cress in the Great Lakes drainage were from 1882 when it was found in western New York (Hill 1909). In the early 1880s, it was also found in the Chicago area, but these records were in the Mississippi drainage basin despite their close proximity (15 to 20 km) to Lake Michigan. The collection of the plant on solid ballast dumping grounds in Mobile, Alabama in 1883, indicates its potential for introduction with solid ballast (Stuckey 1966). Stuckey (1966) suggested that, due to the distance between the Great Lakes populations and those in eastern ports, the introduction of creeping yellow cress into the Great Lakes basin was directly from Europe.

Balsaminaceae

Impatiens glandulifera INDIAN BALSAM

Voss (1985) reported three Michigan records for this Himalayan ornamental plant: from Port

Huron in 1912, Sugar Island in 1956, and on Lake Superior at Grand Marais in 1984. Indian balsam is also known from southwestern Thunder Bay and Thunder Cape on Lake Superior (Soper et al. 1989). Fernald (1950) reported the plant from several northeastern Canadian provinces, including Ontario, and New England. This species is also known to be highly invasive in disturbed or polluted sites in the British Isles (Usher 1986).

Rhamnaceae:

Rhamnus frangula GLOSSY BUCKTHORN

The first records of this European plant in the Great Lakes region are from Ontario prior to 1913 (Britton and Brown 1913). It was collected in Michigan's Delta County in 1934 (Voss 1985). The glossy buckthorn is an aggressive species that is often considered a pest in many habitats (Voss 1985). This deciduous plant was introduced as an ornamental shrub (Bailey 1949).

Onagraceae:

Epilobium hirsutum GREAT HAIRY WILLOW HERB

The first records for this Eurasian marsh species in North America are from Newport, Rhode Island in 1829. Early records show it from cultivated ground and on solid ballast grounds (Stuckey 1970). The first record in the Great Lakes basin are from 1874 near a mill west of Cascadilla Place in Ithaca, New York (Dudley 1886). In 1882 the plant was observed from Clifton, Ontario and later, in 1890, it was collected in Niagara Falls (Stuckey 1970). The Niagara Falls specimens are thought to have been introduced with garden seed. By 1948, the plant had spread further into the Great Lakes basin as far as Cook County, Illinois (Stuckey 1970).

Epilobium parviflorum SMALL FLOWERED HAIRY WILLOW HERB

The earliest known North American record for *Epilobium parviflorum* is from before 1891 on a solid ballast ground at Hoboken, New Jersey (Trelease 1891). It was not reported again until

Purcell (1976) found it in Toronto, Ontario in 1973. On finding the species in Ontario, Purcell examined herbarium specimens of *Epilobium hirsutum* and found many of them to be misidentified specimens of *Epilobium parviflorum*. From this study, eight localities in Ontario were found, the earliest being in 1969 in Midland, Ontario (Purcell 1976). Voss (1985), however, reported *Epilobium parviflorum* in Benzie County, Michigan as early as 1966. The Michigan record is the earliest known collection of the plant in Great Lakes drainage but how the plant was introduced remains unknown (Purcell 1976).

Umbelliferae:

Conium maculatum POISON HEMLOCK

This highly poisonous plant, once valued medicinally as a powerful narcotic was established in eastern North America by the early 1800s (Nuttall 1818, Torrey 1843). By the 1890s, it was established in Michigan (Voss 1985). A native of Europe, poison hemlock is common in waste places, on stream banks, and in other damp areas in the Great Lakes region (Wiegand and Eames 1925, Montgomery 1957 and Voss 1985).

Primulaceae:

Lysimachia nummularia MONEYWORT

In central and western New York, this plant was first reported by Dudley (1886) and Day (1882) and by the 1920s, it had become naturalized throughout the area in ditches and on stream banks (Wiegand and Eames 1925, Zenkert 1934). The plant, a native from Europe, is known to have escaped from gardens in many areas of northeast North America and the Great Lakes basin (Fernald 1950, Swink and Wilhelm 1979).

Lysimachia vulgaris GARDEN LOOSESTRIFE

This ornamental Eurasian plant was first known to escape from cultivation in eastern

Massachusetts between 1867 and 1889 (Gray 1867, Gray 1889). By 1913, it was observed from Maine to Ontario, southern New York and Pennsylvania (Britton and Brown 1913). Although specific locations for the Ontario observations are unknown, they were probably in the Great Lakes drainage since many of the major population centers in Ontario at the turn of the twentieth century were Great Lakes ports. Swink and Wilhelm (1979) noted several large populations in mudflats and shallow water from the Chicago area. Montgomery (1957) noted it as occasionally escaping from cultivation. Zenkert (1934) also records the species from near Buffalo, New York in 1921.

Lythrum salicaria PURPLE LOOSESTRIFE

Thompson et al. (1987) reviewed the introduction and spread of purple loosestrife into North America. Purple loosestrife is thought to have been introduced to Atlantic Coast ports in the early 1800s with imported sheep, in solid ballast, or as a cultivated plant. This wetland species spread rapidly inland thoughout the United States in ballast and other materials and along the New York Erie Canal system. The ecological impacts associated with often monospecific stands of purple loosestrife are their competitive effects on native plants (cattails and other species) and the loss of prime habitat for waterfowl and other marsh animals (Rawinski and Malecki 1984).

Polygonaceae:

Polygonum persicaria LADY'S THUMB

Michaux (1803) notes *Polygonum persicaria* from Kentucky and by 1843 the plant was considered naturalized (Torrey 1843). Native to Europe, the marsh plant is found throughout the Great Lakes basin in a variety of habitats (Day 1882, Dudley 1886, Wiegand and Eames 1925, Zenkert 1934, Montgomery 1957 and Swink and Wilhelm 1979). The mechanism through which it was introduced remains unknown.

Chenopodiaceae:

Chenopodium glaucum OAK LEAVED GOOSE FOOT

Gray (1967) first reported this European plant from city streets and the brackish shores of Onondaga Lake near Syracuse, New York. Since, it has been introduced or expanded into areas throughout the Great Lakes basin and is common in waste places, roadsides, cultivated land, shores and riverbanks, and marshy areas (Day 1882, Wiegand and Eames 1925, Montgomery 1957, Swink and Wilhelm 1979 and Voss 1985). Since it has been found in railroad ballast (Swink and Wilhelm 1979) and along railroad tracks (Wiegand and Eames 1925 and Voss 1985) its spread into and throughout the Great Lakes region was probably mediated by railroads.

Caryophyllaceae:

Myosoton aquaticum GIANT CHICKWEED

Britton and Brown (1913) recorded this European plant from Quebec and Ontario to Pennsylvania. Early Ontario records are from 1894 when the plant was found in Stratford, a town in the Lake St. Clair drainage (Montgomery 1957). Later, it became widely established in southern Ontario where it grew along the Thames River, Rideau River, and Welland Canal and in other areas (Montgomery 1957). Since, the plant has become distributed throughout the Great Lakes basin (Zenkert and Zander 1975, Swink and Wilhelm 1979, Voss 1985). The mechanism through which this plant was introduced remains unknown.

Nymphaceaceae:

Nymphoides peltatum YELLOW FLOATING HEART

The first records of the escape of this European plant from cultivation in North America were in the District of Columbia and in eastern New York (Fassett 1957). It is commonly used in ornamental ponds and garden pools and often gets out of control in nutrient rich pools (Muhlberg 1982). Stuckey (1973) reviewed its North American history and noted that the only known Great Lakes basin record is from 1930 in Ashtabula County, Ohio at the mouth of the Conneaut River.

The current status of this population is unknown (Stuckey 1973).

Boraginaceae:

Myosotis scorpioides TRUE FORGET-ME-NOT

An ornamental plant escaping from cultivation, the European forget-me-not is a common and widespread member of the Great Lakes flora. Early records of the plant in North America date to the earliest floras (Nuttall 1818, Torrey 1824) but later floras note that a native species was misidentified as the European one. By 1867, early records of the European species escaping from gardens were recorded in the Boston area and by 1889 the plant was widely distributed (Gray 1867, 1889). In the Great Lakes drainage the plant is recorded by Dudley (1886) from Ithaca, New York. It is now very common from Lake Superior (Soper et al. 1989) to central New York (Zenkert 1934).

Labiatae:

Lycopus asper WESTERN WATER HOREHOUND

This plant is thought to have been introduced into the Great Lakes from western North America. Stuckey (1969) reviewed the distributional history of *Lycopus asper* in western Lake Erie and Lake St. Clair. Using the wealth of historical botanical data for the region, Stuckey concluded that the *Lycopus asper* populations in the region are nonindigenous. Although records of the plant in other parts of the Great Lakes region are not supported by the historical distributional data that the western Lake Erie data provides, botanists generally agree that the plant has been introduced into the Great Lakes watershed. *Lycopus asper* is thought to have migrated along highway medians and railroad margins in the early 20th century.

Lycopus europaeus EUROPEAN WATER HOREHOUND

The first two North American records for this plant are from Norfolk, Virginia around 1860 and from solid ballast ground in the Delaware River in New Jersey in 1867 (Stuckey and Phillips 1970). Many of the early collections of this plant came from ballast grounds or from port areas. In New York City, the plant was a well documented solid ballast introduction (Brown 1879). In 1903, *Lycopus europaeus* was found in Lake Ontario on Toronto Island. The plant has since spread into the western edge of Lake Erie, through Lake Ontario into the St. Lawrence River (Stuckey and Phillips 1970). The distributional history of the Great Lakes populations indicates that they are not the result of a spread into the watershed from Atlantic populations but represent a separate introduction from Atlantic ports or Europe (Stuckey and Phillips 1970).

Mentha spp. MINTS

Ten species of mint have been introduced into the Great Lakes watershed from Europe. Hybrids between the native and introduced mint species and among the introduced mint species have resulted from these introductions. Because of the hybridizations, the taxonomy of the genus is complex and has changed many times. The introduced mints listed by Fernald (1950) are discussed below. Because of the widespread nature of the their release from cultivation, we have assumed that the plants, as reported in Gray's manual and Britton and Brown (1913) have wider distribution than indicated.

Mentha alopercuroides WOOLLY MINT

This mint is often considered a hybrid of *Mentha rotundifolia* and *Mentha longifolia* (Fernald 1950). Woolly mint was reported by Gray (1889) from Pennsylvania and New Jersey. Britton and Brown (1913) noted additional records from Wisconsin and Missouri but Fernald (1950) did not include these records.

Mentha aquatica WATER MINT

Gray (1867) reported this plant from Delaware and a variety (var. *flabrata*) from Connecticut.

Gray (1889) gave it a distribution from New England to Delaware and New Jersey. Britton and Brown (1913) reported it from Nova Scotia to Pennsylvania and Georgia. Fernald (1950) did not add any Great Lakes records. Although early records for the Great Lakes basin are lacking, Swink and Wilhelm (1979) reported it from several locations near Chicago.

Mentha cardiaca SMALL LEAVED MINT

In Europe, this mint is treated as a hybrid between *Mentha spicata* and *Mentha arvensis* (Fernald 1950). Britton and Brown (1913) reported it from Atlantic coastal states and Fernald (1950) included Michigan, Illinois and Indiana in its distribution.

Mentha citrata BERGAMOT MINT

This mint is often considered a variety of *Mentha aquatica* (Fernald 1950). Britton and Brown (1913) noted the mint from Connecticut to New York, Ohio, Michigan and Missouri. Gray (1889) did not report this mint, so it must have been introduced in the late 1800s.

Mentha crispa CRISPED-LEAVED MINT

Britton and Brown (1913) noted this mint from the east coast. Fernald (1950) added Michigan records to this distribution.

Mentha gentilis CREEPING WHORLED MINT

Gray (1867) noted this mint from river banks in Lancaster Pennsylvania and later (Gray 1889) gave it a distribution from Massachusetts to Pennsylvania. Britton and Brown (1913) described its distribution from Nova Scotia to northern New York, Iowa and North Carolina and Tennessee. Wiegand and Eames (1925) reported the plant as rare and have records from 1915 and 1917 in the Cayuga Lake basin in Central New York. In 1922 and 1924, it had escaped from cultivation in the Buffalo, New York area (Zenkert 1934). This plant is thought to be a hybrid of *Mentha* *spicata* and *Mentha arvensis*, the only native North American mint (Fernald 1950). If this is so, it would account for its rare and sporadic occurrence.

Mentha longifolia HORSE MINT

Gray (1889) noted this mint from Pennsylvania and New Jersey. Britton and Brown (1913) included Ohio in its distribution. Fernald (1950) gave it a distribution from Massachusetts to Indiana, south to Virginia.

Mentha piperita PEPPERMINT

Torrey (1843) reported this mint from moist ground and river shores from the Hudson River and Western New York. Gray (1867) reported that the mint became naturalized quickly because of its use of underground shoots for asexual propagation. Gray (1889) noted that the mint was "everywhere" along brooks.

Mentha rotundifolia ROUND LEAVED MINT

Gray (1867) first reported this species from wet habitat in Cumberland, Maine. In 1924 and 1922, it had escaped from gardens in the Buffalo area (Zenkert 1934). Gray (1889) describes the range of this mint as in coastal states from Maine to Texas. Britton and Brown (1913) noted this mint from Ohio in addition to noting locations from Gray (1889). Fernald (1950) later described the plant from Maine to Michigan.

Mentha spicata SPEARMINT

Torrey (1843) and Gray (1848) noted this species as "perfectly naturalized" in wet meadows and on stream margins. Because the plant was so widespread in 1843, introduction probably occurred long before this date.

Solanaceae:

Solanum dulcamora BITTERSWEET NIGHTSHADE

Early settlers imported this European plant that was becoming naturalized by the early 1800s (Nuttall 1818) in colonial times as a remedy for scurvy and rheumatism (Torrey 1843). The plant is common in lowlands and swamps (Fassett 1957).

Scrophulariaceae:

Veronica beccabunga EUROPEAN BROOKLIME

Veronica beccabunga was first observed in North America in 1876 in Hudson County, New Jersey at the Bergen Tunnel (Les and Stuckey 1985). An early record from solid ballast ground at Hunter's Point, Long Island, New York in 1880, indicated that the plant was introduced in the solid ballast of ocean-going ships arriving from Eurasia. The first observation of European brooklime in the Great Lakes watershed is from Monroe County, New York in Irondequoit in a wet meadow in 1915. The plant is currently distributed in northeastern North America from Michigan and Ohio to the St. Lawrence River in Quebec. Several subspecies of the plant occur. Studies of these species show that the plants present in eastern North America are of the *beccabunga* subspecies which is distributed in Europe (Les and Stuckey 1985).

Compositae:

Cirsium palustre MARSH THISTLE

Britton and Brown (1913) treated the marsh thistle as a species introduced from Europe and only cited one population, in East Andover, New Hampshire. Fernald (1950) indicated that this plant is indigenous to Newfoundland and local but "partly adventive" from Nova Scotia to Northern Michigan. These northern Michigan records most likely represent populations that have migrated or been introduced inland. A. Reznicek of the University of Michigan Herbarium (personal communication, 1990) considers the plant introduced into the marshes around Lake

Superior.

Pluchea purpurescens SALT-MARSH FLEABANE

var. *succulenta*

This variety of *Pluchea purpurescens*, an eastern coastal marsh species, is known in the Great Lakes basin from areas of southern Ontario affected by brine from salt deposits, mines and factories (Catling and McKay 1980), from western New York (Fernald 1950) and from the Chicago area (Swink and Wilhelm 1979). Zenkert (1934) in his *Flora of the Niagara Frontier Region* did not note this plant. He included most of western New York in his survey. The plant was probably introduced into the Great Lakes drainage in western New York between 1933 and 1950.

var. *purpurescens* SALT-MARSH FLEABANE

This variety is known from an area around a salt mine in Michigan near Detroit (Farwell 1916, Fernald 1950). Farwell's (1916) reports of *Pluchea camphorita* from Michigan must have been *Pluchea purpurescens* var. *purpurescens* because the plants are similar and Fernald (1950) cited distributions for *Pluchea purpurescens* var. *purpurescens* in Michigan. Farwell (1916) suggested that these plants were imported with railway freight and survived high salt content in areas adjacent to salt mines.

Solidago sempervirens SEASIDE GOLDENROD

The first inland records for this Atlantic coastal species are from the Chicago area in 1969 (Swink 1969). The plant is common in industrialized parts of Chicago and other areas (Swink and Wilhelm 1979). In 1974, the plant was also found near Windsor, Ontario in areas near salt mines and salt processing plants (Catling and McKay 1980). These two populations represent the only known successfully established inland sites for seaside goldenrod.

Sonchus arvensis FIELD SOW THISTLE

Torrey (1843) noted this aggressive European species from Staten Island, New York near the quarantine area, possibly indicating an introduction with animal bedding or forage. Between 1863 and 1865, the plant was identified from Cayuga Lake, New York and Rochester, New York (Dudley 1886). The plant has become widespread in the Great Lakes basin (Zenkert 1934, Britton and Brown 1913, Deam 1940).

Sonchus arvensis var. *glabrescens* SMOOTH FIELD SOW THISTLE

The earliest records for smooth field sow thistle in the Great Lakes basin are from Erie County, Ohio in 1902 and from Ithaca, New York in 1916 (Long 1922). The taxonomy of these specimens, however, is questionable (Long 1922, Wiegand and Eames 1925). Zenkert (1934) noted that this variety of the European common field sow thistle was most likely "more recently" imported with grain from the northwest into the Buffalo, New York region. It was not included in Britton and Brown (1913). Fernald (1950) noted it from locations throughout Northeastern North America.

H. Algae (Table 10).

Several schools of thought surround the study of introduced algae in the Great Lakes. One viewpoint asserts that the newly discovered algal species in the Lakes were previously rare and uncommon native forms that only appeared in the flora of the Lakes after environmental conditions were altered to favor their increased abundance. The Great Lakes aquatic flora is not well known, for example, 200 diatom species were not yet identified in 1978 (Stoermer and Kries 1978). A second view asserts that the increased salinity and other environmental changes in the Great Lakes has enabled introduced algae often found in marine and brackish environments to more readily adapt to the freshwater habitat.

The algae arrived in the Lakes through a variety of entry mechanisms. All of the introduced diatoms (with the exception of *Thallasiosira pseudonana*) and several other species of algae are thought to have been introduced in the ballast water of ships. Other known mechanisms include accidental releases, ship fouling and canals. We outline below the possible Great Lakes algal introductions.

Ulotrichaceae:

Ulothrix zonata GREEN ALGA

Graham (1982) theorized, through review of evolutionary and cellular studies, that this filamentous green algae native to the Atlantic Coast is a marine form that has invaded the Great Lakes. As evidence, she states that the reproductive mechanisms of the alga, along with those of *Cladophora glomerata* (discussed below) are more similar to the marine species of the class Ulvaphyceae than to related freshwater species (Sheath 1987). *Cladophora* and *Ulothrix* require wave action similar to that of the marine intertidal zone (Sheath 1987). Sheath (1987) noted that the alga did not invade the Lakes recently because it was known from before the early 1900s

(Collins 1928) but concurs with Graham (1982) as to the origin of the species. Introduction mechanisms through which this alga could have been introduced, such as on the hulls of ships or in solid ballast, were present throughout the nineteenth century. *Ulothrix zonata* inhabits the littoral zone above *Cladophora* and *Bangia atropurpurea* (Blum 1982).

Ulvaceae:

Enteromorpha intestinalis f. *maxima* GREEN ALGA

Enteromorpha intestinalis f. *cyindracea* GREEN ALGA

Muenscher (1927) reported the first records of *Enteromorpha intestinalis,* a green alga native to the Atlantic Coast in the Great Lakes drainage from Wolf Creek near Silver Springs, New York in 1926. Taft (1964b) reported collections of *Enteromorpha intestinalis* from the Portage River west of Elmore, Ohio in 1951. The location where he found the algae was on a fault in the limestone bedrock where water was upwelling. Catling and McKay (1980) found these two forms of *Enteromorpha intestinalis* in saline habitat near the Ojibway Salt Mine Near the Detroit River in 1979. They noted that their findings were the first records of this algal species in Ontario. Neither of the forms are noted inland by Collins (1928).

Monostroma bullosum GREEN ALGA

Monostroma wittrockii GREEN ALGA

Monostroma wittrockii, a marine alga native to the Atlantic Coast, was found in the Portage River west of Elmore, Ohio in 1941 (Taft 1946). This was the first known inland record for the alga. The alga was probably introduced accidentally with oyster shells in kitchen waste (Taft 1946). *Monostroma bullosum* also native to the Atlantic Coast was first collected at this Ohio site in 1951 (Taft 1964b). Although Taft (1964b) did not see evidence of the accidental release of *Monostroma bullosum* with discarded seafood, the similar release of this alga is possible. Taft (1964b) noted that the occurrence of this algae in the Portage River was sporadic. *Monostroma* *wittrockii* did not occur after 1941 and *Monostroma bullosum* occurred until 1954. The current status of these algae in the Great Lakes is unknown.

Enteromorpha prolifera GREEN ALGA

Catling and McKay (1980) found this green algae in a pool near a salt factory in Windsor, Ontario in 1979. They noted that this record was the first known occurrence of the alga in Ontario. This algal species, although primarily a marine species, was reported from inland salt springs by Collins (1928).

Cladophoraceae:

Cladophora glomerata GREEN ALGA

Previously considered native, *Cladophora glomerata* is now thought to have been introduced from marine systems (Graham 1982). As in the case of *Ulothrix zonata*, certain reproductive and ecological characteristics indicate that this alga is native to the marine environment. The alga has been known in the Great Lakes system since 1848 when it was noted from all the Lakes except Lake Superior where it was reported in 1871 (Taft 1975). By the 1940s and 1950s, *Cladophora* had become a dominant member of the Great Lakes algal community. In the 1960s and 1970s, beds of *Cladophora* became so extensive that it began fouling lake front property, beaches and swimming areas (Neil 1975). The problems and complaints associated with the *Cladophora* fouling caused considerable scientific and public debate which prompted legislation regulating the release of wastes into the Lakes.

Characeae:

Nitellopsis obtusa GREEN ALGA

The first records of this Eurasian green algae in North America were in 1978 when the plant was found in the St. Lawrence River (Geis et al. 1981). At the time of this study, the plant was found to be present in many sites along the St. Lawrence River from east of Clayton, New York, to east of Ogdensburg, New York (Geis et al. 1981). More recent studies report the alga from the St. Clair-Detroit River system (Schloesser et al. 1986). Ranked as the ninth most frequently collected macrophyte in the St. Clair-Detroit River system, *Nitellopsis* was more frequently observed there than *Potamogeton crispus*, another common Great Lakes exotic. This alga is considered a ballast water introduction.

CHRYSOPHYTA

Hymenomonadaceae:

Hymenomonas roseola COCCOLITHOPHORID

Stoermer and Sicko-Goad (1977) first collected this coccolithophorid in the Great Lakes in Saginaw Bay, Lake Huron in 1975. It normally inhabits eutrophic areas, ponds and small lakes, polluted rivers, and "slightly brackish upper reaches of coastal estuaries" of North America and Europe (Stoermer and Sicko-Goad 1977). *Hymenomonas roseola* was probably introduced in the ballast water of ocean going ships.

Coscinodiscaceae:

Actinocyclus normanii f. *subsalsa* DIATOM

Stoermer and Yang (1969) reported this common European coastal diatom from brackish, silty and polluted waters of Lake Michigan in 1964 and from Lake Erie where it is a dominant summer plankton species. In Europe it occurs in coastal waters of Germany and Norway, the Baltic and Caspian Seas, and freshwaters of Northern Germany (Hasle 1977, 1978).

Biddulphiaceae:

Bidduplhia laevis DIATOM

This diatom, known from lakes and streams in the south and midwest (Weber 1971) and from

North Sea estuaries and the west coast of Africa (Sheath 1987) was not known in the Great Lakes until 1978 when it was observed at the Wyoming water treatment plant on the southern basin of Lake Michigan (Wujek and Welling 1981). This area of Lake Michigan has higher concentrations of chloride ions than other sites in the lake (Wujek and Welling 1981). This diatom comprised 1% the total phytoplankton population during this study (Wujek and Welling 1981). Wujek and Welling (1981) noted the halophyllic nature of this diatom and implicated its introduction to an increase in chloride concentrations in the Lakes. The introduction of this diatom in ballast water is probable. In a survey of the flora and fauna of foreign ballast water entering the Lakes, Bio-Environmental Services Ltd. (1981) identified species of *Biddulphia.*

Terpsinoe musica DIATOM

This diatom, known from "isolated occurrences in American lakes and streams" was not known in the Great Lakes until 1978 when it was observed at the Wyoming water treatment plant on the southern basin of Lake Michigan (Wujek and Welling 1981). It comprised about 4% of the total phytoplankton community. This location in the lake has higher concentrations of chloride ions than other areas of the lake (Wujek and Welling 1981). Wujek and Welling (1981) noted that this is a halophyllic diatom and implicated the increase in chloride concentrations in the Lakes in its introduction and establishment.

Thallasiosiraceae:

Cyclotella atomus DIATOM

Cyclotella atomus is another diatom found in European coastal waters of varied salinity, Java, and South Africa (Nicholls 1981). In Lakes Michigan, Ontario, and Erie the diatom has become common (Nicholls 1981) in localities of "high loadings of dissolved solids (Sheath 1987)." It was collected in 1964 in Lake Michigan (Stoermer and Yang 1969) and is a common component of the sediments of Lake Ontario (Duthie and Sreenivasa 1972). *Cyclotella atomus* is also widespread in North American rivers (Hohn and Hellerman 1963, Weber 1971, Lowe and Busch 1975).

Chaetoceros honii DIATOM

Chaetoceros honii was first described as a new species in Saginaw Bay, Lake Huron in 1978 (Wujek and Graebner 1980). Because the populations were found in areas of high ion content (Wujek and Graebner 1980) and since *Chaetoceros* is generally a marine genus, the species is thought to have originated in a marine or brackish environment (Sheath 1987). The transcontinental introduction of a previously undescribed species in ballast water is a probable explanation for the presence of this diatom in Great Lakes waters. Many non-indigenous species are known to have been first described in the region into where they have been introduced, rather than their native localities (Carlton 1979). Species of *Chaetoceros* non-indigenous to the Great Lakes have been found in surveys of ballast water entering the Great Lakes (Bio-Environmental Services Ltd. 1981).

Skeletonema potamos DIATOM

Hasle and Evensen (1976) noted that this diatom, often mistaken for *Skeletonema subsalsum*, from the Little Miami River near Cincinati, Ohio, where it was first described in 1970, and from Lake Erie and Northern Germany. German collections containing the diatom have been found from as early as 1922. *Skeletonema potamos* has a wide salinity tolerance (Nicholls 1981). The diatom was probably introduced into the Great Lakes from its native range in Europe in the ballast water of ships.

Skeletonema subsalsum DIATOM

The earliest report of this brackish diatom, known from the Baltic Sea, the Caspian Sea and Northern Germany, was in North America in Sandusky Bay, Lake Erie in 1973 (Hasle and Evensen 1975). Stoermer (1978) noted its occurrence in Lake Erie, Lake Ontario, and nearshore areas of Lake Michigan and southern Lake Huron.

Thalassiosira spp.

Four European species of the predominantly marine and brackish genus *Thalassiosira* have been discovered in the Great Lakes since the 1960s. Distributional data for these diatoms is scant, so their native ranges are not accurately known. They are common in Scandinavia, Germany, England and the Baltic Sea (Hasle 1978) and known from the North American Atlantic Coast (Sheath 1987). The species have most likely been transported throughout the world with the ballast water of ships; North American populations could be introduced.

Thalassiosira guillardii DIATOM

The earliest records of *Thalassiosira guillardii* in North America are from Sandusky Bay, Lake Erie in 1973 (Hasle 1978). It has been known from Germany and Sweden since 1910 and also occurs in Yaquina Bay, Oregon (Hasle 1978). Early Great Lake diatom collections either do not contain this diatom, or contain inconclusive fragments (Hasle 1978).

Thalassiosira lacustris DIATOM

Thalassiosira lacustris was first reported from the Great Lakes by Hasle (1978) who noted it from Lake Erie.

Thalassiosira pseudonana DIATOM

The earliest reported collections of *Thalassiosira pseudonana* are from 1973 from Miller Blue Hole, Ohio, an artesian well in the Lake Erie drainage (Lowe and Busch 1975). Stoermer (1978) reported the diatom from Lake Michigan, Lake Ontario, Lake Erie, and from areas less than 10 km from the Lakes. Because of the obscurity of the localities where this diatom is found (e.g. an artesian well) the mechanism of introduction remains unknown.

Thalassiosira weissflogii DIATOM

Hasle (1978) noted the synonymy of *Thalassiosira fluviatilis* Hust and *Thalassiosira weissflogii* G. Fryx. & Hasle. The earliest reports of *Thalassiosira fluviatilis* are from the Detroit River in 1962-1963 (Wujek 1967). Stoermer and Yang (1969) reported it from Lake Michigan in 1967.

PHAEOPHYTA

Sphacelariaceae:

Sphacelaria fluviatilis BROWN ALGA

Sphacelaria lacustris BROWN ALGA

Sphacelaria, a genus of brown algae generally considered marine, was first observed in the Great Lakes watershed when *Sphacelaria fluviatilis* was found in Gull Lake, Michigan, which drains into Lake Michigan (Thompson 1975, Timpano 1978). Prior to this Great Lakes record, the only reported occurrence of *Sphacelaria fluviatilis* was from western China (Jao 1943). The transport mechanism of *Sphacelaria fluviatilis* remains unknown. Soon after, in 1975, the brown alga *Sphacelaria lacustris* was first described in Lake Michigan (Schloesser and Blum 1980). As in the case of *Chaetoceros honii*, *Sphacelaria lacustris* could be a previously undescribed ballast introduction. Sheath (1987) notes, as in the case of other marine algal invaders, the freshwater populations are not known to undergo sexual reproduction, indicating that the populations did not evolve independently of the marine environment. The unexpected occurrences of these algal species in Lake Michigan waters and their lack of sexual reproduction prompted Sheath (1987) to consider the genus nonindigenous to the Great Lakes basin.

RHODOPHYTA

Bangiaceae:

Bangia atropurpurea RED ALGA

This filamentous red alga native to the Atlantic Coast was observed in Lake Erie in 1964 (Lin and Blum 1977). After this sighting, records for Lake Ontario (Damann 1979), Lake Michigan (Weik 1977), Lake Simcoe (Jackson 1985) and Lake Huron (Sheath 1987) were reported. It has become a major species of the littoral flora of these lakes, generally occupying the littoral zone with *Cladophora* and *Ulothrix* (Blum 1982). Earliest records of this algae in the basin, however, go back to the 1940s when Smith and Moyle (1944) found the alga in Lake Superior tributaries. Matthews (1932) found the alga in Quaker Run in the Allegheny drainage basin. Smith and Moyle's records must have not resulted in spreading populations since the alga was not known in Lake Superior as of 1987. Kishler and Taft (1970) were the most recent workers to refer to the records of Smith and Moyle (1944) and Matthews (1932). The prevailing belief is that this alga was transferred to the lower Great Lakes through ship fouling or ballast water.

Goniotrichaceae:

Chroodactylon ramosum RED ALGA

This red alga, native to the Atlantic Ocean, was first reported in the Great Lakes from western Lake Erie by Taft (1964a). An epiphyte on *Cladophora*, it is found in the Lakes from Lake Ontario to Lake Huron (Sheath and Morison 1982). The St. Lawrence River does not have the wave action to support the growth of *Choodactylon ramosum* (Sheath and Morison 1982), so its natural migration up the river from the Atlantic is unlikely. The alga probably arrived in the ballast water of ships.

VI. Discussion

A. Summary

Since the early 1800s 136 organisms have been introduced into the Great Lakes (Figure 1). The majority of these species are aquatic plants (45%), fish (18%) and algae (18%). The mollusks, oligochaetes, crustaceans, flatworms, bryozoans, cnidarians and disease pathogens each have represented less than 10% of the nonindigenous species in the Great Lakes.

Exotic organisms have entered the Great Lakes basin through a variety of vectors (Figure 2). These include unintentional releases, introductions related to ships, deliberate releases, entry through or along canals, and movement along railroads and highways. We attempted to determine the most probable entry vector for each species, but in some cases vectors were either unknown (17%) or we were not able to distinguish between several mechanisms (e.g. multiple mechanism category) (16%). Purple loosestrife, for example, could have invaded the Great Lakes either along canals, highways or railroads, in the solid ballast of ships or a combination of the three. Consequently, we have included purple loosestrife under the multiple mechanism category in Figure 2. Likewise, 22 additional exotic organisms were included in the multiple mechanism category. The most common entry vectors within the multiple entry mechanism (Figure 3) and for all Great Lakes species in general (Figure 2) were unintentional releases and releases associated with ships. Canals, railroad or highway migration and deliberate releases individually make up less than 10% of the entry mechanisms. Although only a small percentage of the organisms have arrived through canals (Figures 2 and 3), several of them (e.g. the sea lamprey, alewife and white perch) have caused some of the most significant impacts on Great Lakes resources.

The most commonly utilized release mechanisms, unintentional releases represent 37% of the exotic species introduced in the Great Lakes (Figures 2 and 3). Within this category, 47% of the introductions are escapees from cultivation (Figure 4). Accidental releases (28%), introductions associated with fish stocking or bait (15%), and aquarium releases (10%) have also made significant contributions in this category.

Shipping activities have played a significant role in the transfer of non-native species and represent the second most commonly utilized mechanism used by non-native species to enter the Great Lakes (Figures 2 and 3). Within this category, 56% of the introductions have been linked to ships' ballast water, 34% have arrived in solid ballast and 10% were brought into the Lakes on the hulls of ships (Figure 5).

Since the 1800s, as human activity and the extent of introduction mechanisms in the Great Lakes basin increased, the rate of introduction of exotic species has also increased (Figure 6). Over one third of the nonindigenous species in the Great Lakes have been discovered in the past 30 years. When introductions are classified by entry mechanism over time (Figure 7), the role of ship-related activities in the recent transport of organisms has become more evident. Since 1959, the bulk of the exotic species entering the Great Lakes have been related to shipping activities. This surge in ship related introductions has coincided with the opening of the St. Lawrence Seaway. Historically, ships have also played an important role in the transfer of aquatic organisms, particularly in the late 1800s with the release of aquatic plants in solid ballast materials. In general, for all Great Lakes exotic species, since the early 1800s: 1) deliberate releases have declined, 2) canal migrations have remained consistently low, 3) railroad and highway migrations have been sporadic and 4) unintentional releases have been consistently high (Figure 7).

Most exotic species in the Great Lakes have come from Europe (47%), the Atlantic Coast (18%) and Eurasia (14%) (Figure 8). The large number of introductions from Europe and Eurasia are most likely associated with (1) the settlement of the Great Lakes basin by Europeans who transported goods primarily from Europe and (2) the similarity of the climate of the Great Lakes region and Europe. While most exotic species in the Great Lakes are European in origin, several species (sea lamprey, alewife, white perch, some of the salmonids and *Cladophora*) migrating from the North American Atlantic Coast and other U.S. drainages have had significant ecological and economic impacts.

B. Impacts of exotic organisms in the Great Lakes

One of the most pervasive and perhaps the least appreciated anthropogenic effects on the world's aquatic ecosystems is the global transfer of exotic organisms. Such transfers of exotic species to new environments may lead to extensive ecological alterations to the structure of pre-invasion communities. These alterations may arise through a wide variety of processes, including (but not limited to) interspecific competition, disturbance, and predation. Many of these processes have been deduced through the correlation of the arrival of an exotic species and the subsequent alteration (in terms of numbers and/or distribution) of a native species; far fewer have been tested through experimentation. Exotic species may also have broad economic (and other social) impacts on the human communities which have historically relied upon the now-altered resources (such as food stocks and raw water supplies). Here we consider nine groups of organisms and provide an overview of their significant environmental effects.

Of the 136 species treated here, we know little about how most of these "fit" into the modern-day structure of Great Lakes communities. As a consequence, we know little or nothing, for most of these taxa, about how these communities may have changed after their arrival. Of the total exotic biota, about ten percent of these species (as discussed below) have had demonstrably significant impacts on the Lakes. Of the fish about fifty percent have been shown to have important ecological and/or economic effects. An erroneous conclusion would be that about fifty percent of the introduced fish have been ecologically inconsequential, or that ninety percent of the invasions overall have had little or no ecological impact. We emphasize here that the apparent lack of effects may be due to a variety of factors, including (1) that easily observed alterations in community structure may predate modern investigations by decades or centuries, such that experimental manipulations would be required to elucidate any historical interactions and (2) that the effects may simply not have been studied.

The ecological and economic impacts of the introduced fish species have been large. Of the twenty four introduced fish species in the Lakes nearly half have had significant effects (both positive and negative). Some of the earliest introductions of nonindigenous fish species have had long-term impacts. The extension of the sea lamprey's range since the 1830s has been associated with the decline of several fish species and has caused millions of dollars in damage to the sport and commercial fisheries on the Lakes (Fetterolf 1980), and millions of dollars continue to be spent on control. Costs of lamprey control will continue to be high. When the alewife was first introduced into the Lakes, predators were not sufficiently abundant to check its population growth. Consequently periodic dieoffs of the alewife polluted shores and blocked the intake pipes of water treatment plants and other industries. While the alewife suppressed the coregonines, yellow perch, emerald shiners, and rainbow smelt it subsequently became an important prey fish for introduced salmon, and the system has come into fragile "balance" (Emery 1985).

The stocking of rainbow trout, chinook salmon, and common carp began in the 1870s. These introductions were intended to augment the declining commercial food fishes of the Atlantic Coast (e.g. American shad and Alantic salmon) and the Great Lakes (lake whitefish and lake trout). Carp never became popular and by the 1890s was considered a problem because of its impacts on habitat used by waterfowl and more favored fish species. The salmonids, whether introduced deliberately into the Lakes to enhance the sport fishery or unintentionally as in the case of the pink salmon, have had profound and permanent ecological effects on the fish fauna. Through competition, predation, and habitat alteration, the introduced salmonids have impacted native salmonid species both ecologically and genetically (Krueger and May 1991).

The effects of the white perch, one of several fish that entered the Great Lakes through the Erie Canal, are difficult to assess (Christie 1973, Hurley 1986), but the potential for competition with native species remains high (Elrod et al. 1981, Schaeffer and Margraf 1986). Recently, the European ruffe has established a population in the St. Louis River in Duluth Harbor in Lake Superior. This population has reached very high densities and is expanding its range. The ruffe may become a major competitor with other species throughout the Lakes.

While the intentional, legal introduction of nonindigenous fish species in the Lakes has declined, unintentional, illegal, and ballast water releases continue to occur. We assume that the risks to the Great Lakes resources will continue to be high as long as non-native members of this group continue to gain entry to the Lakes.

Mollusks introduced into the Great Lakes have had and will continue to have a major impact. After its introduction in the 1870s, *Bithynia tentaculata*, commonly known as the faucet snail, spread throughout the basin and often occurred in high densities (Baker 1901b). By the 1900s, the snail had begun to infest municipal water supplies, from intake pipes to household faucets (Baker 1902). The arrival of the zebra mussel *Dreissena polymorpha* in 1986 has set the stage for potential long term changes to the structure of pelagic and benthic communities in the Great Lakes and to the economic and social future of lake users. It is the major fouling organism in the Great Lakes of water intakes and nautical and littoral structures (Griffiths et al. 1989) and is expected to lead to billions of dollars in control costs. As a major filterer of the water column, the zebra mussel may lead to significant changes to both pelagic systems (in terms of the removal of plankton and other suspended materials) and benthic systems (in terms of seston deposition and the rapid transfer of nutrients to bottom communities). As a benthic species, the zebra mussel occupies vast areas of primary space but also provides secondary vertical structure. Zebra mussel fouling on private vessels and structures and thick shell deposition on beaches may have social consequences in terms of those who use the Lakes as a recreational resource. The zebra mussel is expected to expand into other North American waters because of its planktonic larval stage (unusual for a freshwater bivalve) and its ability to be passively transported as veligers and as adults by over a score of dispersal vectors, including currents, vessels and bait buckets (Carlton 1991).

The ecological impacts of the introduced crustaceans, oligochaetes, bryozoans, cnidarians and flatworm are not known. The recently introduced spiny water flea, a predatory cladoceran, has recently undergone rapid expansion in the Great Lakes, but its ecological impact is not expected to be great (Sprules et al. 1990). Historically, the ecological and economic risks associated with these groups have not been as high as those of other taxa.

Only two fish disease pathogens have been introduced, those causing salmonid whirling disease and furunculosis. Problems associated with these diseases have mainly occurred in fish hatcheries. The concentration of fish and the regular introduction of fish into these facilities makes them vulnerable to outbreaks of disease (Bullock et al. 1983, Wolf and Markiw 1985).

Introduced plant species (61) outnumber all other groups of introduced organisms. While the impact of most plants is not known, several, such as purple loosestrife and Eurasian watermilfoil, have had significant impacts in the Great Lakes basin. Purple loosestrife often inhabits marshland in monospecific stands, out-competing native cattails and other plants and making these areas less suitable as wildlife habitat (Rawinski and Malecki 1984). It has spread throughout the Great Lakes basin. The arrival of Eurasian watermilfoil has also had a significant impact in Lakes within the Great Lakes basin. Massive beds of the plant often impair the use of boats and make the Lakes undesirable for other recreational uses. Because the potential for the introduction of problem-causing plants is high (e.g. the water chestnut in the Hudson River) future introductions of aquatic plants should be of concern.

The ecological impacts of the majority of the introduced algal species in the Great Lakes are not known. *Cladophora glomerata*, however, has had both ecological and economic impact. *Cladophora* did not reach its peak abundance until the 1940s and 1950s when it became a dominant member of the littoral algal community. In the1960s and 1970s, the alga's abundance reached problematic proportions when it began fouling lake front property, beaches and swimming areas (Shear and Konasewich 1975). The debate over the causes of the problems associated with *Cladophora* and other algae encouraged the governments of the United States and Canada to sign the Great Lakes Water Quality Agreement in 1972 which stipulated measures to reduce the release of nutrients and waste into the Great Lakes.

Of the organisms we have highlighted above, we have identified 14 (~10%) that have had what we consider the greatest impacts (both positive and negative) on the Great Lakes. These include *Cladophora*, sea lamprey, alewife, purple loosestrife, chinook salmon, brown trout, common carp, coho salmon, furunculosis, whirling disease, white perch, Eurasian watermilfoil, zebra mussel and ruffe (Figure 9). Of these, four were deliberately introduced into the Lakes while the remainder were associated with either canals, railroads and highways, ships, or unintentional releases.

Historically, the non-indigenous species with the greatest impacts in the Great Lakes have entered the basin in two distinct periods. In the mid-to-late 1800s a peak of introductions coincided with the establishment of organisms associated with canals, ships solid ballast and the initial deliberate release of several fish species. A second surge which occurred from 1933 until 1990, included ship ballast water species, species associated with renewed fish stocking efforts in the Lakes, a canal introduction and an unintentional release.

The ecological and economic impacts of exotic species in the Great Lakes have been and will continue to be enormous. Even though only a fraction of the impacts of the species introduced into the Lakes have been individually significant, all the species have contributed to the artificial character of the Great Lakes. Introduced species exist at almost every level of the food chain of the Great Lakes and the changes brought about by these organisms have damaged the natural community of the Lakes. Finally, as long as the Great Lakes are subject to human-mediated transfer mechanisms and environmental problems like global climate change, the largest freshwater resource in the world will continue to be at risk from the invasion of exotic species.

VII. Conclusions

1. One-hundred thirty six non-indigenous aquatic species have been identified as established in the Great Lakes. These species are represented by aquatic plants, fish, algae, mollusks, oligochaetes, crustaceans, disease pathogens, bryozoans, cnidarians, and flatworms, most of which have come from Europe (47%), the Atlantic Coast (18%), and Eurasia (14%)

2. The Great Lakes have been subject to invasions by aquatic species since the early 1800s. With increased human activity in the Great Lakes watershed, the rate of introductions have increased over the past two centuries. Over one-third of the introductions have occurred in the last 30 years, a period which coincides with the opening of the St. Lawrence Seaway in 1959.

3. Great Lakes exotic species have arrived through a variety of mechanisms including unintentional releases, releases associated with ships, deliberate releases, migration through and along canals, and migration along railroads and highways. Unintentional releases (37%) and releases associated with ships (32%) are the two most commonly utilized entry vectors of Great Lakes exotic species.

4. Although all non-indigenous species have contributed to the artificial community of the Great Lakes, nearly 10 percent of the species have had significant economic and ecological impacts on Great Lakes resources.

VIII. Acknowledgements

This study was spurred on by the enthusiasim of many individuals who made significant contributions to the success of the research. The following is a list of individuals who provided invaluable information and contributed in a team effort toward development of a comprehensive analysis of exotic species introductions in the Great Lakes basin: A.G. Ballert, R. Brinkhurst, E. Crossman, R. Dirig, M. Dochoda, D. Dodge, L. Emery, J. Farrell, J. Forney, J. Gannon, D. Green, R. Herman, H. Hobbs III, R. Horner, D. Jennings, D. Jude, G. Mackie, J. Magnuson, T. Nalepa, K. Nichols, B. Peckarsky, R. Sheath, T. Reynoldson, A. Reznicek, A. Robertson, D. Schloesser, W. Spalding, R. Sparks, J. Stanley, L. Straub, D. Stryer, W. Stuckey, E. Woltman, and W. Youngs. Special thanks go to William Taylor, chairman of the Great Lakes Fishery Commission Board of Technical Experts and to both Marg Dochoda and Randy Eshenroder who provided the stimulus and support to initiate this project. Finally, this project would not have been successful without the funding support of the Great Lakes Fishery Commission.

Table 1. Location abbreviations for sitings 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
Unknown	U

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

Family	Species	Common Name	Origin	Date	Location	Mechanism
Petromyzontidae	*Petromyzon marinus*	sea lamprey	Atlantic	1830s	Lake Ontario	C, S(F)
Clupeidae	*Alosa pseudoharengus*	alewife	Atlantic	1873	Lake Ontario	C, R(F)
Salmonidae	*Oncorhynchus gorbuscha*	pink salmon	Pacific	1956	Current River, Ont. (S)	R(A)
	Oncorhynchus kisutch	coho salmon	Pacific	1933	Lake Erie	R(D)
	Oncorhynchus nerka	kokanee	Pacific	1950	Lake Ontario (t)	R(D)
	Oncorhynchus tshawytsch	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	Pere Marquette R., MI (M)	R(D)
					Genessee River, NY (O)	R(A)
Osmeridae	*Osmerus mordax*	rainbow smelt	Atlantic	1912	Crystal Lake (M)	R(D), C
Cyprinidae	*Carrassius auratus*	goldfish	Eurasia	≥1878	widespread	R(AQ),R(D), R(A)
	Ctenopharyngodon idella	grass carp	Asia	1974	Lake Michigan drainage	R(D)
	Cyprinus carpio	common carp	Eurasia	≤1879	widespread	R(D)
	Notropis buchanani	ghost shiner	Mississippi	1979	Thames River (StC)	R(F)
	Scardinius erythrophthalmus	rudd	Europe	1989	Lake Ontario	R(F)
Cobitidae	*Misgurnus anguillicaudatus*	Oriental weatherfish	Asia	1958	Shiawassee River (H)	R(A)
Ictaluridae	*Noturus insignis*	margined madtom	Atlantic	1928	Oswego River (O)	C, R(F)
Poeciliidae	*Gambusia affinis*	western mosquitofish	Mississippi	1923	Cook Co. Illinois (M)	R(D)
Gasterosteidae	*Apeltes quadracus*	fourspine stickleback	Atlantic	1986	Thunder Bay (S)	S(BW)
Moronidae	*Morone americana*	white perch	Atlantic	1950	Cross Lake (O)	C
Centrarchidae	*Lepomis humilis*	orangespotted sunfish	Mississippi	1929	Lake St. Mary's (E)	U
	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 (StC)	S(BW)
	Proterorhinus marmoratus	tubenose goby	Eurasia	1990	St. Clair River (StC)	S(BW)

Table 4. Origin, date and location of first sighting, and entry mechanism(s) for non-indigenous mollusks in the Great Lakes (For location and introduction mechanism codes see Tables 1 and 2).

Family	Species	Common Name	Origin	Date	Location	Mechanism
Gastropoda:						
Lymnaeidae	*Radix auricularia*	European ear snail	Eurasia	1901	Chicago (M)	R(A), A(AQ)
Viviparidae	*Cipangopaludina chinensis malleata*	Oriental mystery snail	Asia	1931	Niagara River (O)	R(AQ)
	Cipangopaludina japonicus	Oriental mystery snail	Asia	1940s	Lake Erie	R(D)
Valvatidae	*Valvata piscinalis*	European valve snail	Europe	1897	Lake Ontario	S(SB)
Bithyniidae	*Bithynia tentaculata*	faucet snail	Europe	1871	Lake Michigan	S(SB), R(D)
Pelecypoda:						
Sphaeriidae	*Sphaerium corneum*	European fingernail clam	Eurasia	<1962	Lakes Erie, Ontario	U
	Pisidium amnicum	greater European pea clam	Europe	1897	Genesee River (O)	S(SB)
Corbiculidae	*Corbicula fluminea*	Asiatic clam	Asia	1980	Lake Erie	S(F), R(A), R(F), R(AQ)
Dreissenidae	*Dreissena polymorpha*	zebra mussel	Europe	1988	Lake St. Clair	S(BW)

Table 5. Origin, date and location of first sighting, and entry mechanism(s) for non-indigenous crustaceans in the Great Lakes (For location and introduction mechanism codes see Tables 1 and 2).

Family	Species	Common Name	Origin	Date	Location	Mechanism
Cladocera:						
Cercopagidae	*Bythotrephes cederstroemi* (BC)	spiny water flea	Europe	1984	Lake Huron	S(BW)
Bosminidae	*Eubosmina coregoni*	water flea	Europe	1966	Lake Michigan	S(BW)
Copepoda:						
Temoridae	*Eurytemora affinis*	calanoid copepod	Atlantic	1958	Lake Ontario	S(BW)
Diaptomidae	*Skistodiaptomus pallidus*	calanoid copepod	Mississippi	1967	Lake Ontario	R(A), R(F)
Amphipoda:						
Gammaridae	*Gammarus fasciatus*	gammarid amphipod	Atlantic	U	U	S(BW), S(SB)

Table 6. Origin, date and location of first sighting, and entry mechanism(s) for non-indigenous oligochaetes in the Great Lakes (For location and introduction mechanism codes see Tables 1 and 2).

Family	Species	Common Name	Origin	Date	Location	Mechanism
Lumbriculidae	*Stylodrilus heringianus*	oligochaete	Europe	1962	North Channel St. Mary's River	U
Naidae	*Ripistes parasita*	oligochaete	Europe	1980	North Channel	S(BW)
Tubificidae	*Branchiura sowerbyi*	oligochaete	Asia	1951	Kalamazoo River (M)	R(A)
	Phallodrilus aquaedulcis	oligochaete	Europe	1983	Niagara River (O)	S(BW)
	Potamothrix bedoti	oligochaete	Eurasia	1918	Cayuga Lake (O)	U
	Potamothrix vejdovskyi	oligochaete	Eurasia	1963	Lake Erie	U
	Spirosperma ferox	oligochaete	Europe	1962	Lake Ontario	U

Table 7. Origin, date and location of first sighting, and entry mechanism(s) for non-indigenous fish disease pathogens in the Great Lakes (For location and introduction mechanism codes see Tables 1 and 2).

Taxon	Species	Common Name	Origin	Date	Location	Mechanism
Bacteria	*Aeromonas salmonicida*	furunculosis	U	1937	U	R(F)
Protozoa	*Myxosoma cerebralis*	salmonid whirling disease	U	1968	Ohio (E)	R(F)

Table 8. Origin, date and location of first sighting, and entry mechanism(s) for other non-indigenous invertebrates in the Great Lakes (For location and introduction mechanism codes see Tables 1 and 2).

Taxon	Species	Common Name	Origin	Date	Location	Mechanism
Platyhelmenthes	*Dugesia polychroa*	flatworm	Europe	1968	Lake Ontario	S(BW)
Bryozoa	*Lophopodella carteri*	bryozoan	Asia	1933	Lake Erie	R(A), R(AQ), S(BW or SB)
Cnidaria	*Cordylophora lacustris*	hydroid	widespread	1956	Lake Erie	U
Cnidaria	*Craspedacusta sowerbyi*	freshwater jellyfish	Asia	1933	Lake Erie (t)	R(A)

Table 9. Origin, date and location of first sighting, and entry mechanism(s) for non-indigenous aquatic plants in the Great Lakes (For location and introduction mechanism codes see Tables 1 and 2).

Family	Species	Common Name	Origin	Date	Location	Mechanism
Marsileaceae	*Marsilea quadrifolia*	European water fern	Europe	<1900	Cayuga Lake, NY (O)	R(D)
Typhaceae	*Typha angustifolia*	narrow leaved cattail	Atlantic	<1882	Central NY (O)	RH
Sparganiaceae	*Sparganium glomeratum*	bur reed	Europe	1941	Lake Superior	U
Zosteraceae	*Potamogeton crispus*	curly pondweed	Eurasia	1879	Keuka Lake (O)	R(F), R(D)
Najadaceae	*Najas marina*	spiny naiad	Eurasia	1864	Onondaga Lake (O)	U
	Najas minor	minor naiad	Europe	1935	Cayuga Lake (O)	R(D)
Butomaceae	*Butomus umbellatus*	flowering rush	Europe	1918	Detroit River (E)	S(SB)
Hydrocharitaceae	*Hydrocharis morsus-ranae*	European frog-bit	Europe	1979	St. Lawrence River (O)	R(C)
Gramineae	*Echinochloa crusgalli*	barnyard grass	Europe	<1824	widespread	S(SB)
	Glyceria maxima	reed sweet-grass	Europe	1940	Ontario (O)	R(C), S(SB)
	Poa trivialis	rough-stalked meadow grass	Europe	<1840s	Cayuga Lake basin (O)	R(C), S(SB)
	Puccinella distans	weeping alkali grass	Eurasia	<1925	Montezuma, NY (O)	S(SB), RH
Cyperaceae	*Carex acutiformis*	swamp sedge	Europe	1951	St. Joseph Lake (M)	U
	Carex disticha	sedge	Europe	1866	Bellleville, Ontario (O)	S(SB)
	Carex flacca	sedge	Eurasia	1896	Detroit River (E)	S(SB)
Juncaceae	*Juncus compressus*	flattened rush	Eurasia	1895	Cayuga Lake (O)	R(A)
	Juncus gerardi	black-grass rush	Atlantic	1862	Chicago (M)	S(SB)
	Juncus inflexus	rush	Eurasia	1936	Hancock Mich. (S)	U
Iridaceae	*Iris pseudocorus*	yellow flag	Europe	1886	Cayuga Lake, NY (O)	R(C)
Salicaceae	*Salix alba*	white willow	Europe	≤1848	widespread	R(C)
	Salix fragilis	crack willow	Europe	≤1848	widespread	R(C)
	Salix purpurea	purple willow	Europe	≤1848	widespread	R(C)
Betulaceae	*Alnus glutinosa*	black alder	Europe	1900s	wideaspread	R(C)
Myricaceae	*Myriophyllum spicatum*	Euasian water milfoil	Eurasia	1960	Lake Ontario	S(BW), R(AQ)
Polygonaceae	*Rumex longifolius*	dock	Europe	1901	Isle Royal (S)	U
Cruciferae	*Nasturtium microphyllum*	water cress	Europe	1913	Ithaca, NY (O)	R(C)
	Nasturtium officinale	water cress	Europe	1847	Niagara Falls, NY (O)	R(C)
	Rorippa sylvestris	creeping yellow cress	Europe	1882	Western NY (O)	S(SB)
Balsaminaceae	*Impatiens glandulifera*	Indian balsam	Asia	1913	Port Huron (StC)	R(C)
Rhamnaceae	*Rhamnus frangula*	glossy buckthorn	Europe	<1913	Ontario	R(C)
Onagraceae	*Epilobium hirsutum*	great hairy willow herb	Eurasia	1874	Ithaca, NY (O)	R(A), S(SB)
	Epilobium parviflorum	small flowered hairy willow herb	Europe	1966	Benzie Co. MI (M)	U
Umbelliferae	*Conium maculatum*	poison hemlock	Europe	<1840s	widespread	R(C)
Primulaceae	*Lysimachia nummularia*	moneywort	Europe	1882	western NY (O)	R(C)
	Lysmachia vulgaris	garden loosestrife	Europe	<1913	widespread	R(C)
	Lythrum salicaria	purple loosestrife	Europe	1869	Cayuga Lake (O)	C, S(SB)

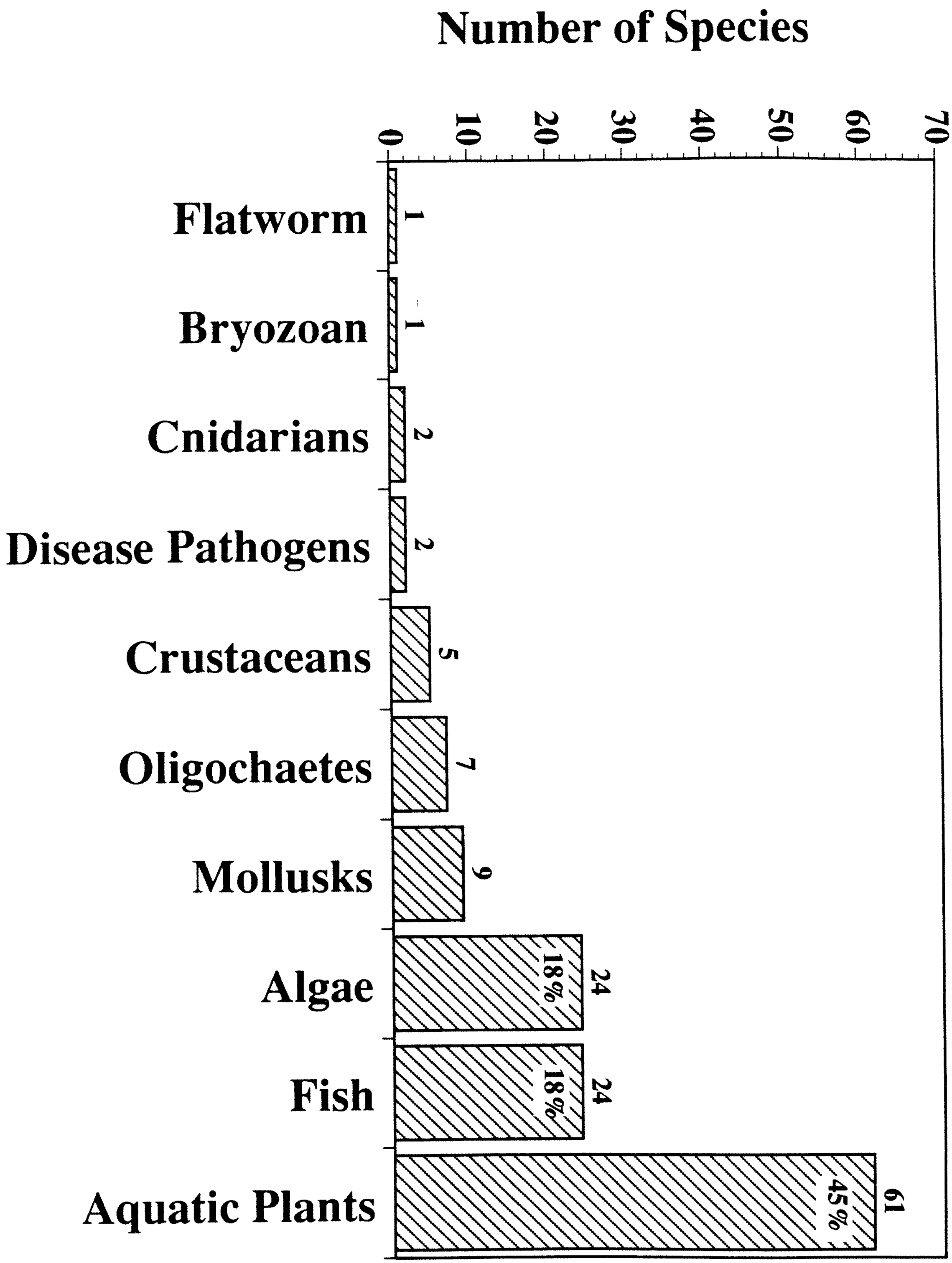
Table 9 (Continued). Origin, date and location of first sighting, and entry mechanism(s) for non-indigenous plants in the Great Lakes (For location and introduction mechanism codes see Tables 1 and 2).

Family	Species	Common Name	Origin	Date	Location	Mechanism
Polygonaceae	*Polygonum persicaria*	lady's thumb	Europe	<1843	widespread	U
Chenopodiaceae	*Chenopodium glaucum*	oak leaved goose foot	Europe	1867	Onondaga Lake, NY (O)	RH
Caryophyllaceae	*Myosoton aquaticum*	giant chickweed	Europe	1894	Stratford, Ontario (StC)	U
Menyanthaceae	*Nymphoides peltatum*	yellow floating heart	Europe	1930	Conneaut R. (E)	R(C)
Boraginaceae	*Myosotis scorpioides*	true forget-me-not	Europe	1886	Ithaca (O)	R(C)
Labiatae	*Lycopus asper*	western water horehound	West	1900s	western Great Lakes (S)	RH
	Lycopus europaeus	European water horehound	Europe	1903	Toronto Isle (O)	S(SB)
Labiatae	*Mentha alopercuroides*	woolly mint	Europe	late 1800s	widespread	R(C)
	Mentha aquatica	water mint	Europe	1979	widespread	R(C)
	Mentha cardiaca	small leaved mint	Europe	<1950	widespread	R(C)
	Mentha citrata	bergamot mint	Europe	late 1800s	widespread	R(C)
	Mentha crispa	crisp-leaved mint	Europe	<1950	widespread	R(C)
	Mentha gentilis	creeping whorled mint	Europe	1915	Central New York (O)	R(C)
	Mentha longifolia	horse mint	Europe	late 1800s	widespread	R(C)
	Mentha piperita	peppermint	Europe	<1843	western NY	R(C)
	Mentha rotundifolia	round leaved mint	Europe	early 1900s	widespread	R(C)
	Mentha spicata	spearmint	Europe	<1843	widespread	R(C)
Solanaceae	*Solanum dulcamora*	bittersweet nightshade	Europe	<1818	widespread	R(C)
Scrophulariaceae	*Veronica beccabunga*	European brooklime	Europe	1915	Monroe Co., NY (O)	S(SB)
Compositae	*Cirsium palustre*	marsh thistle	Eurasia	1913-1950	N. Mich/NY	U
	Pluchea purpurescens					
	var. succulenta	salt-marsh fleabane	Atlantic	<1950	western NY	U
	var. purpurescens	salt-marsh fleabane	Atlantic	<1916	Michigan (E)	R(A)
	Solidago sempervirens	seaside goldenrod	Atlantic	<1969	Chicago (M)	U
	Sonchus arvensis	field sow thistle	Europe	1863	Ithaca (O)	R(A)
	Sonchus arvensis var. glabrescens	smooth field sow thistle	Europe	1902	Erie Co, Ohio (E)	R(A)

Table 10. Origin, date and location of first sighting, and entry mechanism(s) for non-indigenous algae in the Great Lakes (For location and introduction mechanism codes see Tables 1 and 2).

Family	Species	Common Name	Origin	Date	Location	Mechanism
Chlorophyta:						
Ulotrichaceae	*Ulothrix zonata*	green alga	Atlantic	U (1800s)	U	S(F), C
Ulvaceae	*Enteromorpha intestinalis f. cylindracea*	green alga	Atlantic	1926	Wolf Creek (O)	U
	Enteromorpha intestinalis f. maxima	green alga	Atlantic	1926	Wolf Creek (O)	U
	Enteromorpha prolifera	green alga	Atlantic	1979	Lake St. Clair	U
	Monostroma bullosum	green alga	Atlantic	1951	Portage R. (E)	R(A)
	Monostroma wittockii	green alga	Atlantic	1941	Portage R. (E)	R(A)
Cladophoraceae	*Cladophora glomerata*	green alga	Atlantic	U (1800s)	U	S(F), C
Characeae	*Nitellopsis obtusa*	green alga	Europe	1983	Lake St. Clair	S(BW)
Chrysophyta:						
Hymenomonadaceae	*Hymenomonas roseola*	coccolithophorid	NA and Europe	1975	Lake Huron	S(BW)
Coscinodiscaceae	*Actinocyclus normanii f. subsalsa*	diatom	Europe	1964	Lake Michigan	S(BW)
Biddulphiaceae	*Biddulphia laevis*	diatom	Europe	1978	Lake Michigan	S(BW)
Anaulaceae	*Terpsinoe musica*	diatom	Atlantic	1978	Lake Michigan	S(BW)
Thallasiosiraceae	*Chaetoceros honii*	diatom	marine	1978	Lake Huron	S(BW)
	Cyclotella atomus	diatom	NA and Europe	1964	Lake Michigan	S(BW)
	Skeletonema potamos	diatom	Europe	1970	Lake Erie	S(BW)
	Skeletonema subsalsum	diatom	Europe	1973	Lake Erie	S(BW)
	Thalassiosira guillardii	diatom	Europe	1973	Lake Erie	S(BW)
	Thalassiosira lacustris	diatom	Atlantic	<1978	Lake Erie	S(BW)
	Thalassiosira pseudonana	diatom	Atlantic	1973	Miller Blue Hole (E)	U
	Thalassiosira weissflogii	diatom	Europe	1962	Detroit River (E)	S(BW)
Phaeophyta						
Sphacelariaceae	*Sphacelaria fluviatilis*	brown alga	Asia	<1975	Gull Lake, Mich.	U
	Sphacelaria lacustis	brown alga	U	1975	Lake Michigan	S(BW)
Rhodophyta						
Bangiaceae	*Bangia atropurpurea*	red alga	Atlantic	1964	Lake Erie	S(F), S(BW)
Goniotrichaceae	*Chroodactylon ramosum*	red alga	Atlantic	<1964	Lake Erie	S(BW)

List of Figures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Mollusks
Algae
Fish
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7
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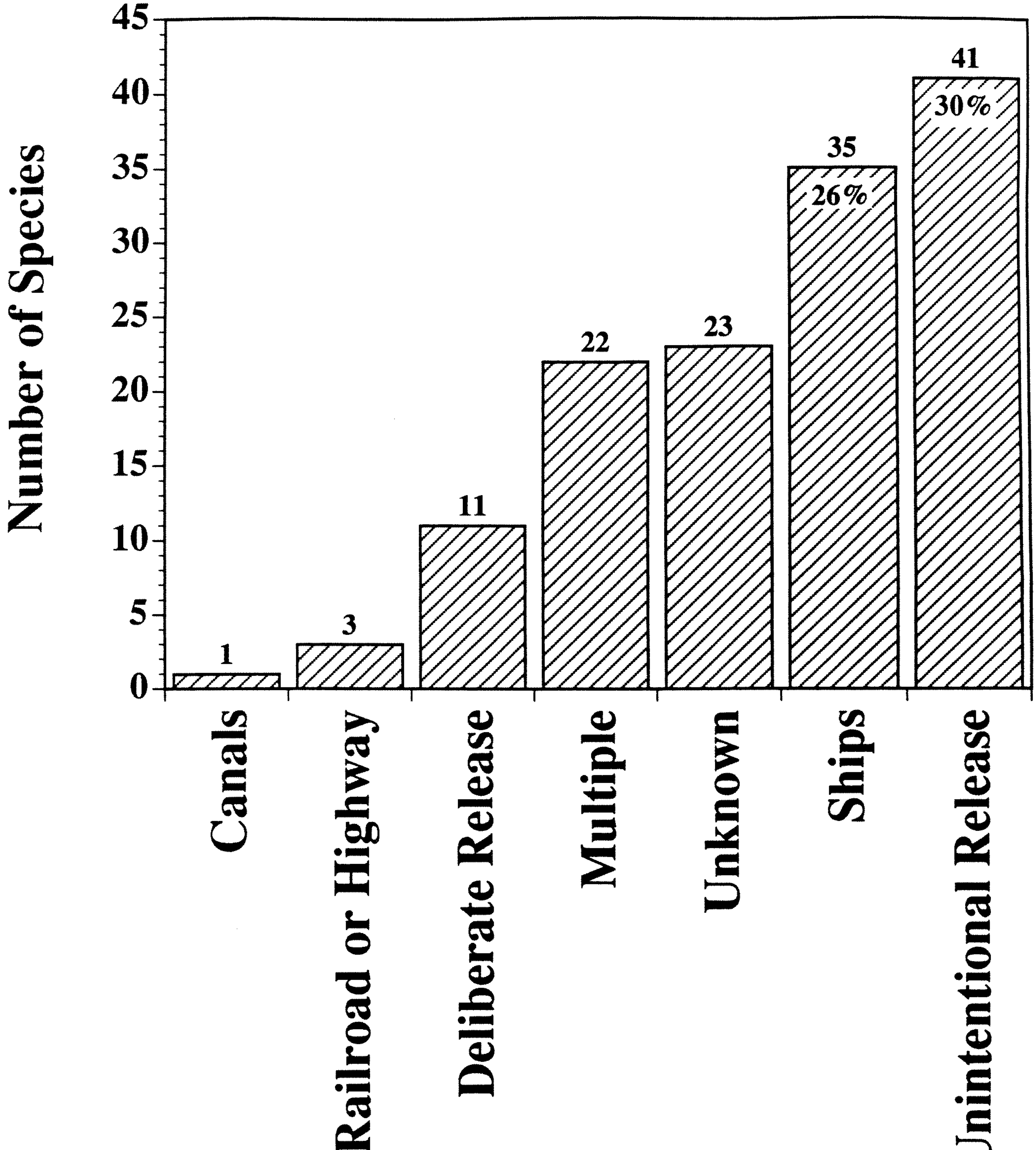
18%
24
18%
61
45%

Figure 1

Figure 2



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Deliberate Release
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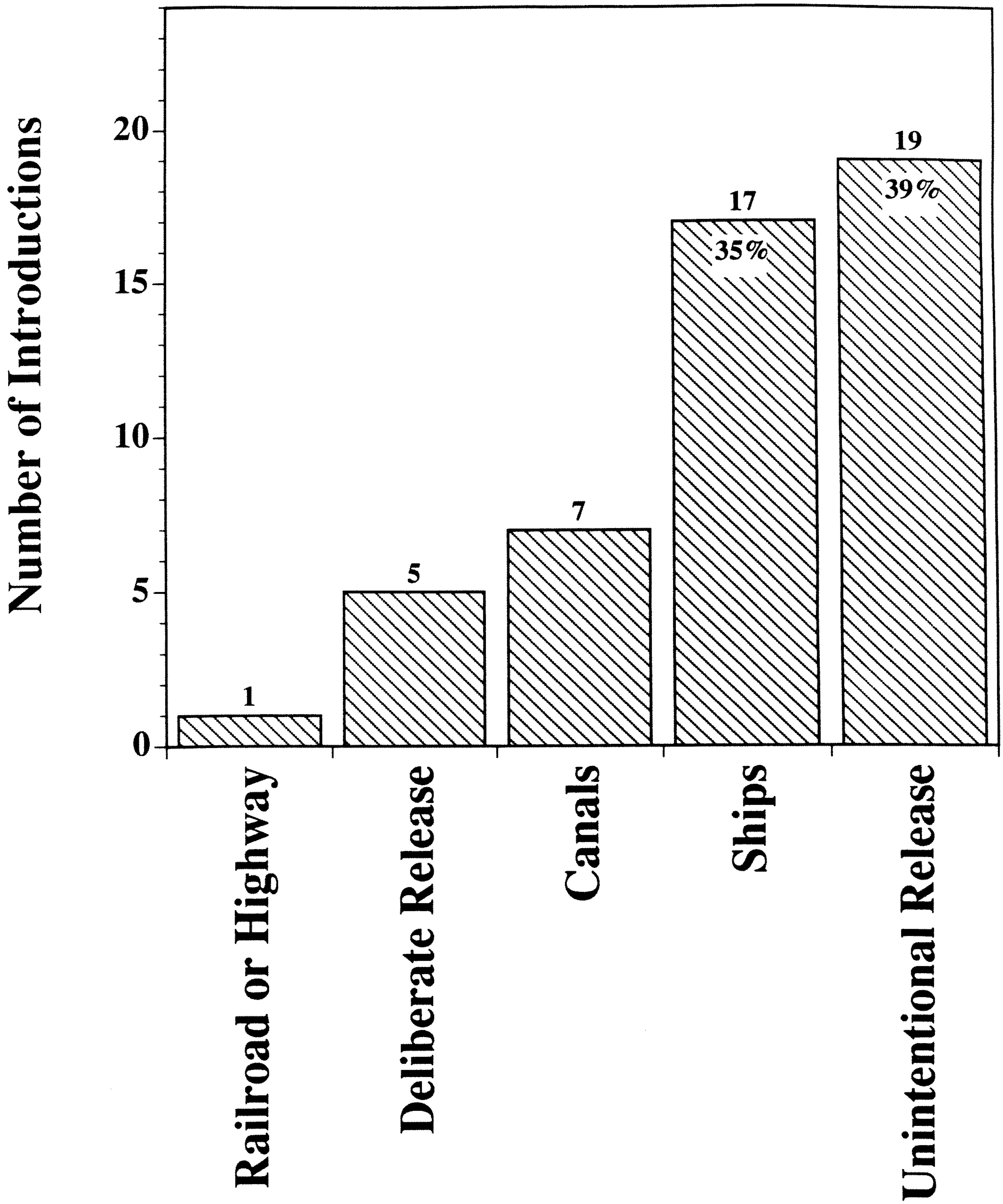
Ships
Unintentional Release

Figure 3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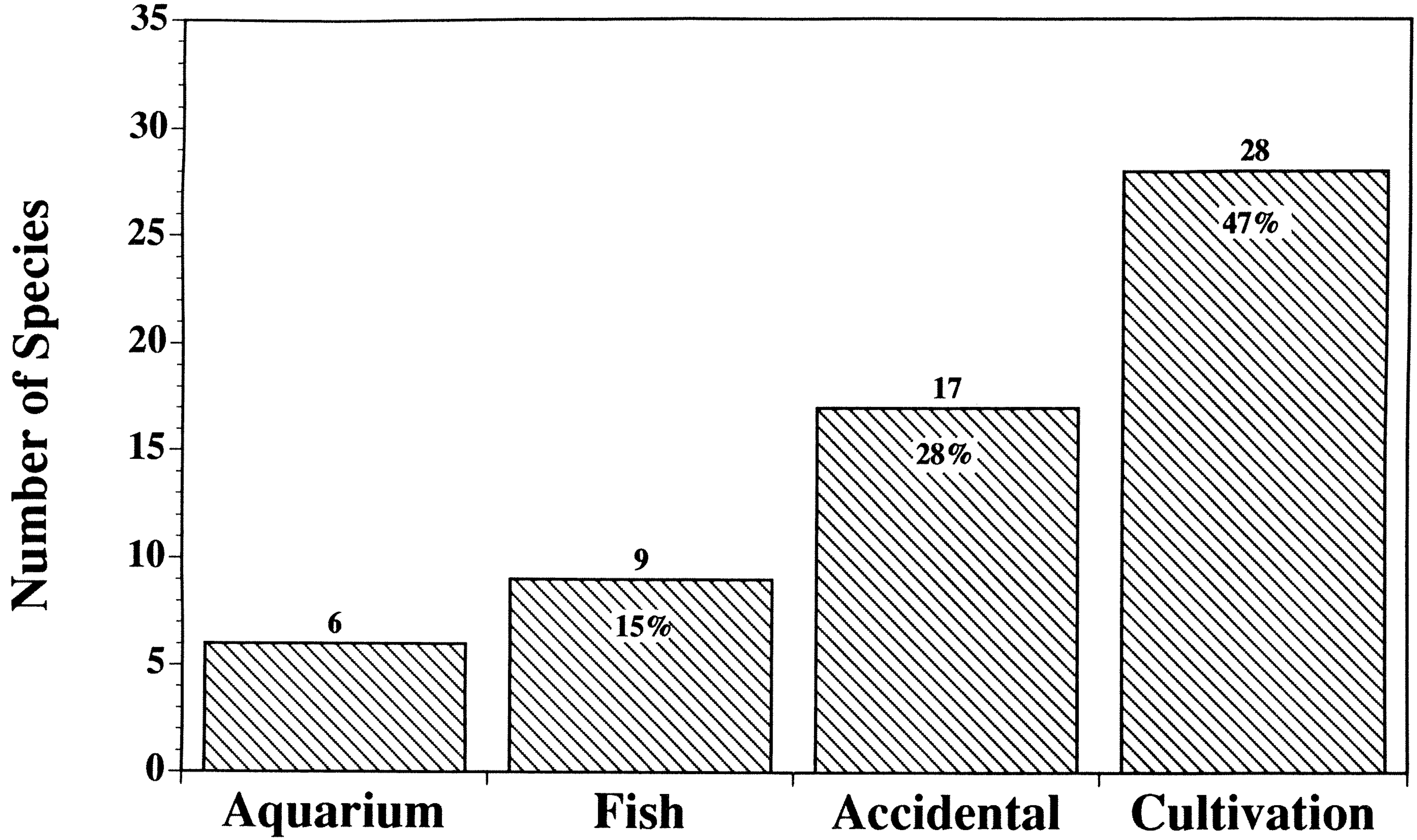
Railroad or Highway
Deliberate Release
Canals
Ships
Unintentional Release

Figure 4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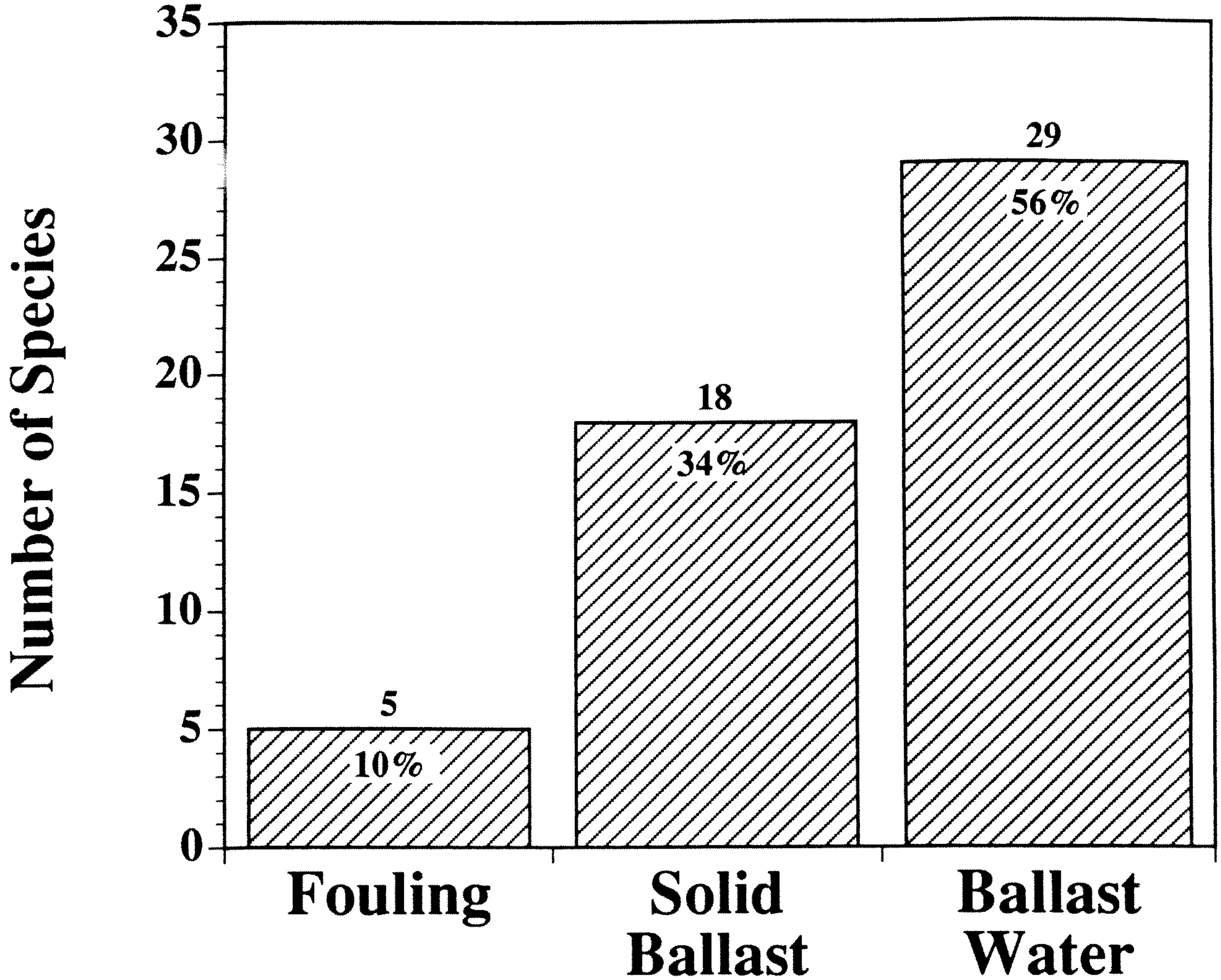
Aquarium
Fish
Accidental
Cultivation

Figure 5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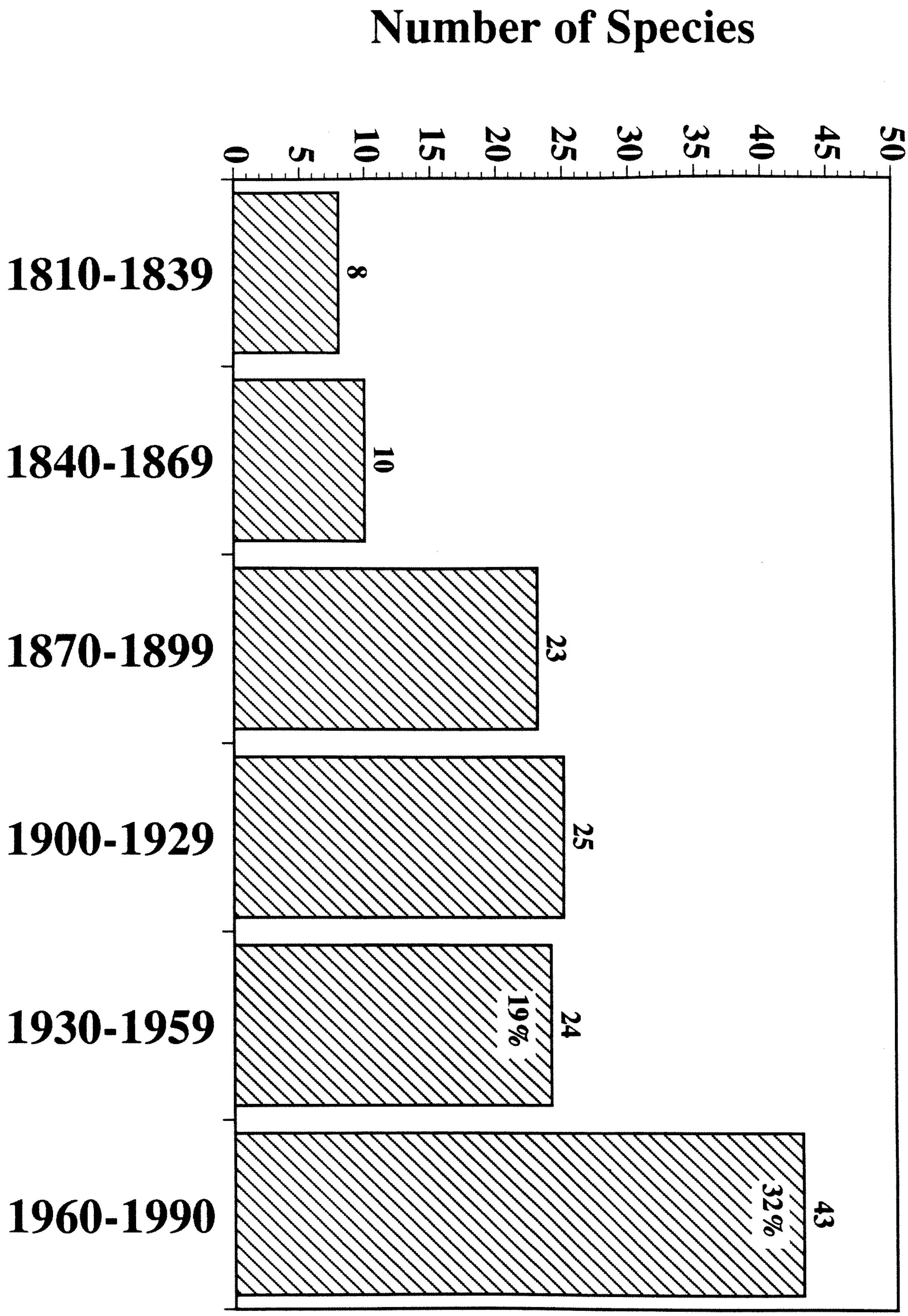
Solid Ballast
Ballast Water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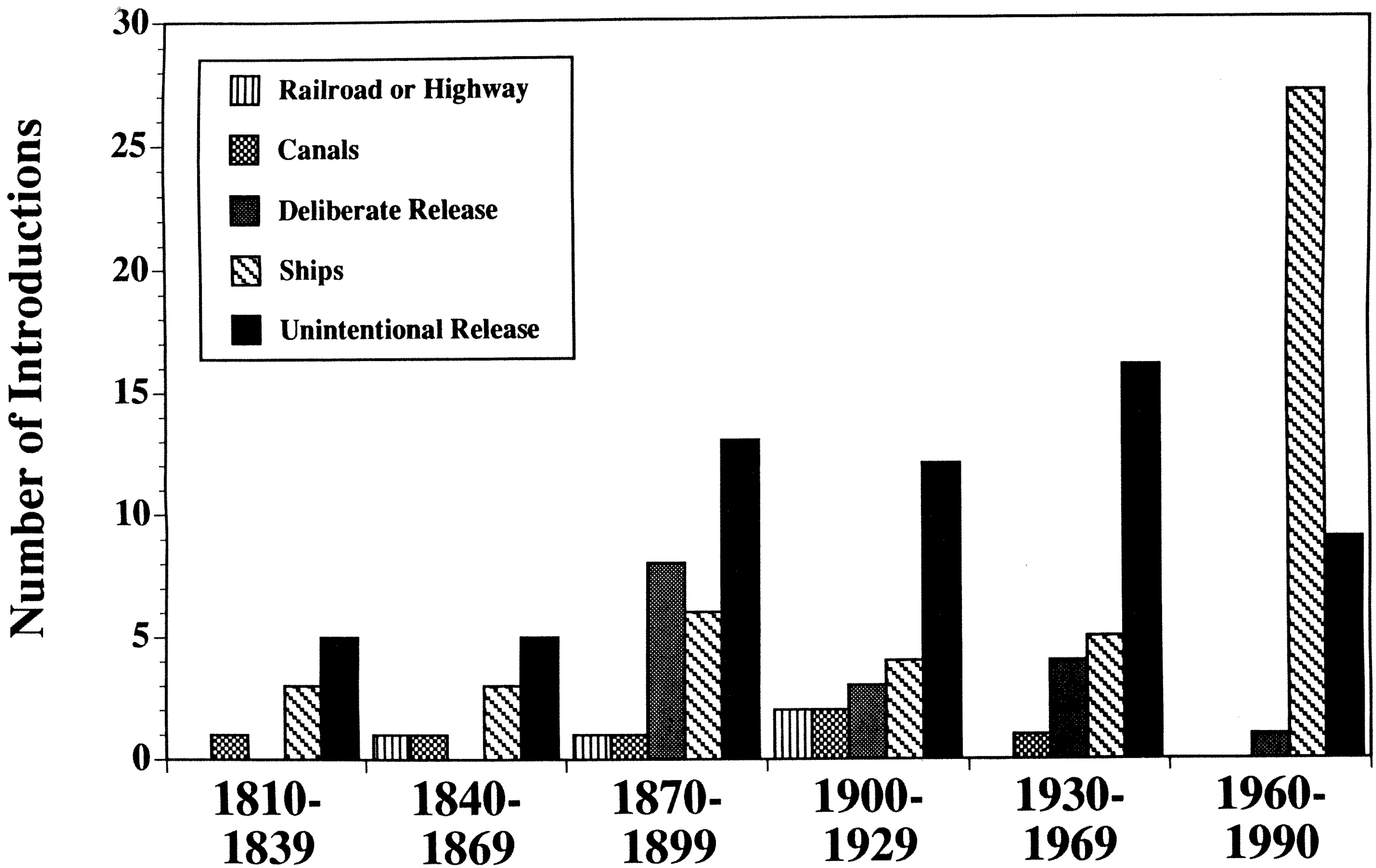
25
30
35
40
45
50
1810-1839
1840-1869
1870-1899
1900-1929
1930-1959
1960-1990
8
10
23
25
24
19%
43
32%

Figure 6

Figure 7



Number of Introductions
30
25
20
15
10
5
0
Railroad or Highway
Canals
Deliberate Release
Ships
Unintentional Release
1810-1839
1840-1869
1870-1899
1900-1929
1930-1969
1960-1990

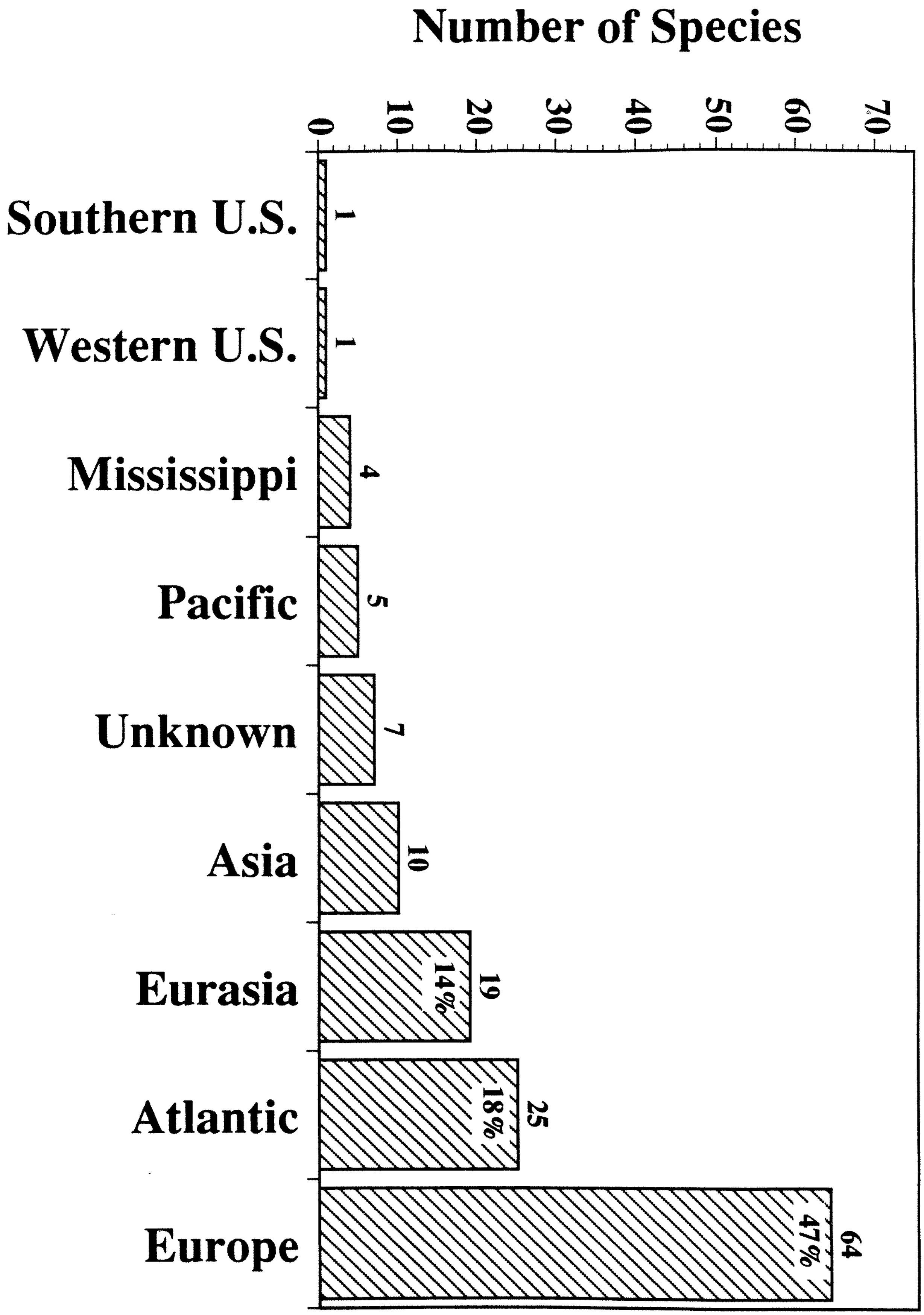
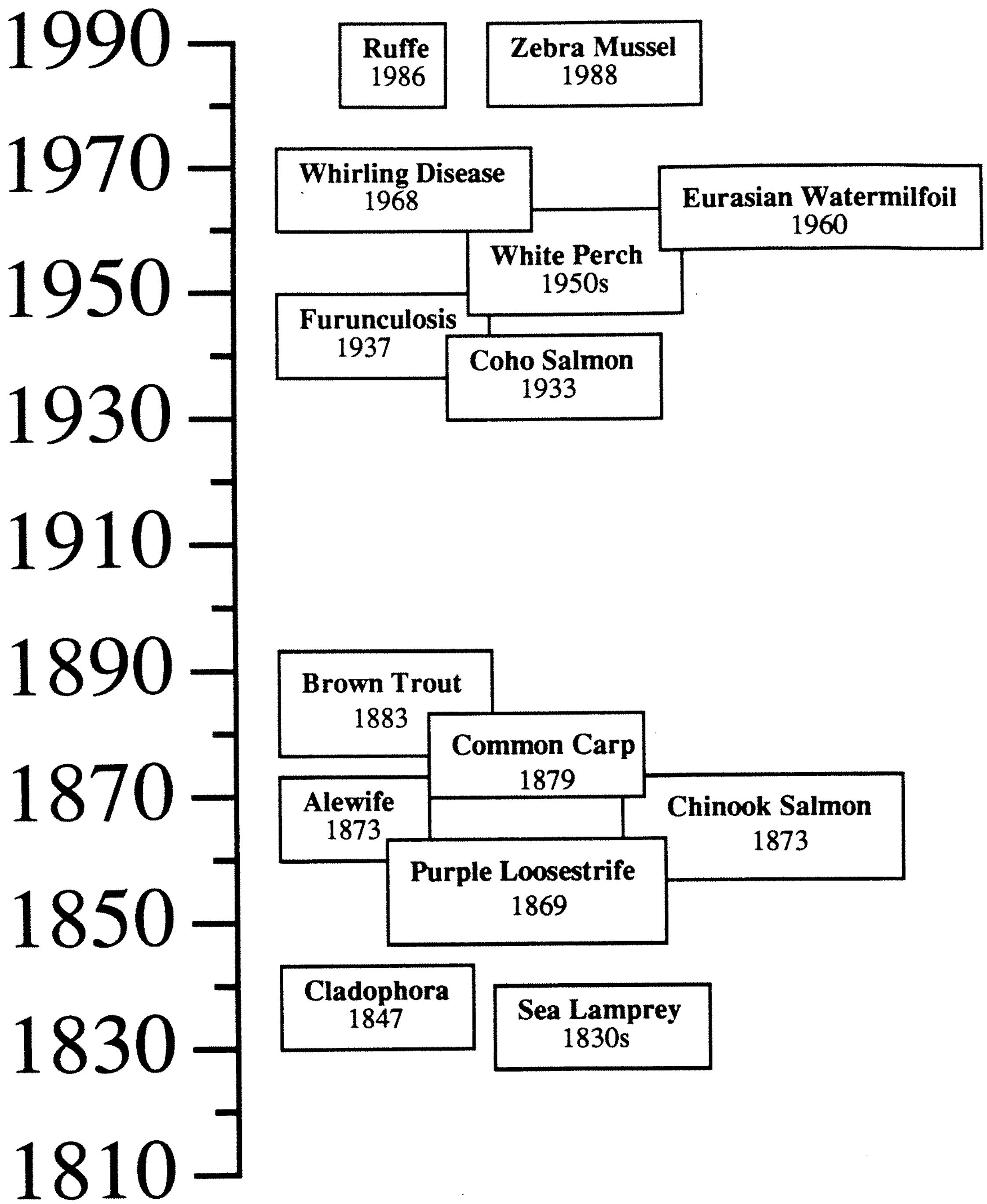

Number of Species
0
10
20
30
40
50
60
70
Southern U.S.
1
Western U.S.
1
Mississippi
4
Pacific
5
Unknown
7
Asia
10
Eurasia
19
14%
Atlantic
25
18%
Europe
64
47%

Figure 8

Figure 9


1990
1970
1950
1930
1910
1890
1870
1850
1830
1810
Ruffe 1986
Zebra Mussel 1988
Whirling Disease 1968
Eurasian Watermilfoil 1960
White Perch 1950s
Furunculosis 1937
Coho Salmon 1933
Brown Trout 1883
Common Carp 1879
Alewife 1873
Chinook Salmon 1873
Purple Loosestrife 1869
Cladophora 1847
Sea Lamprey 1830s

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