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Review

Recent history of nonindigenous species in the Laurentian Great Lakes; An update to Mills et al., 1993 (25 years later)

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ABSTRACT

The seminal work of Mills et al. (1993) lists 137 established aquatic species as nonindigenous to the Great Lakes (two plants are further subdivided into two subspecies groups). We have removed seven of these species: three have been redefined as probably native, and four plants (including both subspecies of *Sonchus arvensis*) have been reclassified as terrestrial. Thirty-five species that arrived prior to 1993 (some due to reclassification, some due to a time lag in discovery and reporting) have been added to the list. Twenty-four new species have become established post-1993, bringing the total to 188 (with *Pluchea odorata* including two subspecies). Notably, 21 of the 23 species were introduced between 1993 and 2006, but only 3 new species have been documented with new reproducing and overwintering populations in the last decade. Multiple revisions have been made to taxonomy and introduction dates based on additional review of literature and museum/herbarium collections. Over the most recent 25 years, the rate of introduction of nonindigenous species capable of becoming established has declined. With the 2006 expansion of ballast regulations to include residual ballast sediments in vessels declaring 'No Ballast on Board', the rate of new invasions has fallen to a low of only 0.25 species per year.

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Introduction

The Great Lakes are host to thousands of native fishes, invertebrates, plants, and other species that not only provide recreational and economic value to the region, but also hold important ecological value. However, with over 180 documented aquatic nonindigenous species and an invasion rate estimated at 1.3–1.8 species·year^{-1}, the Great Lakes basin is considered one of the most heavily invaded aquatic systems in the world (GLRI Task Force, 2010; Mills et al., 1993; Ricciardi, 2006). Some of these nonindigenous species may become invasive (i.e. "those species whose introduction does or is likely to cause economic or environmental harm or harm to human health" (Executive Order 13112, 1999)) and threaten the ecological and/or socio-economic value of the Great Lakes. Understanding the patterns and processes involved in the introduction of nonindigenous species at a comprehensive regional scale is a necessary foundation to prevent harm to the regional economy and environment.

In 1993, Mills et al. (1993), hereafter Mills, published a comprehensive review of the nonindigenous flora and fauna of the Great Lakes basin, documenting 139 nonindigenous aquatic organisms (137 species, two of which include two subspecies) that had become established in the Great Lakes since the early 1800s. They reported on the taxonomy, origin, and most probable entry mechanisms (vector) for each of these species. Beginning in 2003, the National Oceanographic Atmospheric Administration (NOAA) used this list as the core of the Great Lakes Aquatic Nonindigenous Species Information System (GLANSIS: https://www.glerl.noaa.gov/

glansis/), tracking these species and providing public access to information on their distributions, ecology, and management.

In the 25 years since Mills, many additional species have invaded the Great Lakes, and several taxonomic revisions have taken place. Ricciardi (2001) added substantially to the list of Great Lakes nonindigenous species in the course of examining the invasion meltdown hypothesis. Grigorovich et al. (2003a, 2003b) created a list of ballast-mediated animal introductions that added to the overall count. Ricciardi (2006) also provided a major update to Mills and reanalysis of some trends in 2006. Here, we provide a comprehensive update to the inventory and reanalysis of the trends and patterns which Mills observed in light of more recent events, including regulation of ballast carried by transoceanic vessels: ballast exchange requirements on the Great Lakes started in 1993 pursuant to the Nonindigenous Aquatic Nuisance Prevention and Control Act with an exemption for vessels declaring 'No Ballast on Board' (NOBOB), and saltwater flushing of residual ballast sediments in NOBOB vessels was required starting in 2006.

Methods

Data repository

All primary distribution data used in this analysis has been incorporated into the Great Lakes Aquatic Nonindigenous Species Information System (GLANSIS) and is publicly available via GLANSIS. GLANSIS operates as a regional node of the USGS Nonindigenous Aquatic Species database using data specific to the Great Lakes region. The Great Lakes data in the system is maintained and updated by NOAA and USGS staff using quality control protocols which meet or exceed the standards of both agencies. GLANSIS acts as an aggregator of quality-controlled data from a wide variety of sources and includes documentation of the original source for each record. This analysis is based on the earliest available records for each species within GLANSIS and the original source for each of these records is documented in the Results section if they differ from Mills.

Definitions and criteria

Mills defined exotic species as "successfully reproducing organisms transported by humans into the Great Lakes, where they did not previously exist." We more rigorously define 'established nonindigenous species' based on four criteria, which were developed with input from an expert review panel composed of Great Lakes invasion biologists (convened ca. 2001).

Geographic criterion: Only species that are established in the Great Lakes basin below the ordinary high water mark – including connecting channels, wetlands and waters ordinarily attached to the Great Lakes – are included. Species that have invaded inland lakes within the Great Lakes basin, which do not meet the above geographic criterion, are not included. Species that have been found only in ballast tanks are not included.
Aquatic criterion: We include only aquatic species. USDA wetland indicator status is used as a guideline for determining whether wetland plants should be included in the list – Obligate, Facultative Wetland, and Facultative plants are included in this list as aquatic; Facultative Upland and Upland plants are not. Amphibians, reptiles, aquatic mammals and waterfowl, which spend only a portion of their life in the water, are not included.
Nonindigenous criterion: The species included in GLANSIS are those that are considered nonindigenous within the Great Lakes basin and meet at least three of the following definitions and criteria (based on Ricciardi, 2006):

1. The species appeared suddenly and had not been recorded in the basin previously.
2. It subsequently spreads within the basin.
3. Its distribution in the basin is restricted compared with native species.
4. Its global distribution is anomalously disjunct (i.e. contains widely scattered and isolated populations).
5. Its global distribution is associated with human vectors of dispersal.
6. The basin is isolated from regions possessing the most genetically and morphologically similar species.

Established criterion: Kočovský et al. (2018) highlight the particular importance that must be placed on defining the word 'established', which has taken on a variable meaning in the literature. For our purposes, a nonindigenous species is considered established if it has an overwintering and reproducing population within the basin, as inferred from multiple discoveries of adult and juvenile life stages over at least two consecutive years. Given that successful establishment may require multiple introductions, species are excluded if their records of discoveries are based on one or a few non-reproducing individuals whose occurrence may reflect merely transient species or unsuccessful invasions (examples include pacu, flounder, alligators, etc., but data on such introductions are not collected systematically). Dates and locations of observation of each nonindigenous species in the Great Lakes were determined from a combination of peer-reviewed literature, grey literature (agency reports), and personal communications with expert confirmation. In recent years, a number of museums have begun digitizing their collections (e.g., herbarium and specimen records), and in many cases these have resulted in revision of 'earliest dates'. Although we only include species that have become established below the ordinary high water mark and for which reproduction is confirmed, the 'earliest date' is the date of first collection for the watershed, usually resulting in 'first dates' that are significantly earlier than the date at which the species is added to the database.

We followed the protocol of Mills in determining probable vectors and geographic sources for each species. Their protocol was largely based on review of the literature, knowledge of the organisms' biology and ecology, knowledge of their native and introduced ranges, as well as recent studies examining the prevalence of organisms in transit in particular vectors.

Results

Fishes

There are now 28 species of nonindigenous fish established in the Great Lakes. Mills listed 25 species, two of which (*Noturus insignis and Notropis buchanani*) have been removed from this list due to new information indicating that they are likely native to a portion of the Great Lakes, though these should still be considered to be expanding their ranges within the region. Five new species (*Alosa aestivalis*, *Esox niger*, *Ictiobus bubalus*, *Lepisoteus platostomus*, and *Pylodictis olivaris*) have been added. Additional revisions have been made to 'first sighting' dates and locations for several fishes based on re-examination of historical collections and recent literature (Table 1). Below, we provide changes since Mills in information on previous introductions and the new nonindigenous species. We present this in chronological order; if a species is not featured in this section, then there are no updates.

Table 1
Origin, date and location of first sighting, and vector(s) for nonindigenous aquatic fish of the Great Lakes.

Species	Common name	Origin	Date	Location	Vector
Petromyzon marinus[b]	Sea lamprey	Atlantic	1863	Lake Ontario	Canal, ship fouling
Alosa pseudoharengus[b]	Alewife	Atlantic	1868	Cayuga Lake	Canals, release with fish
Oncorhynchus tshawytscha[b]	Chinook salmon	Pacific	1870	Lake Huron	Deliberate release
Oncorhynchus mykiss	Rainbow trout	Pacific	1876	Lake Huron	Deliberate release
Carassius auratus[b]	Goldfish	Asia	1880	Lake Huron	Aquarium release, release with fish, unintentional release
Cyprinus carpio[b]	Common carp	Asia	1880	Huron	Deliberate release
Salmo trutta	Brown trout	Eurasia	1883	Lakes Ontario and Michigan	Unintentional release & deliberate release
Pylodictis olivaris[a]	Flathead catfish	Mississippi River	1890	Lake Erie	Canal, unintentional release & deliberate release
Osmerus mordax[b]	Rainbow smelt	Atlantic	1906	Northern Lake Michigan	Deliberate release
Enneacanthus gloriosus[b]	Bluespotted sunfish	Atlantic	1916	Oneida	Aquarium release, release with fish, canals
Gambusia affinis[b]	Western mosquitofish	Mississippi	1923	Cook Co., Illinois	Deliberate release
~~*Noturus insignis*~~	~~Margined madtom~~	~~Atlantic~~	~~1928~~	~~Oswego River~~	~~Canals, release with fish~~
Lepomis microlophus	Redear sunfish	Southern U.S.	1928	Inland Indiana	Deliberate release
Lepomis humilis	Orangespotted sunfish	Mississippi	1929	Lake St. Mary's	Canals
Scardinius erythrophthalmus[b]	Rudd	Eurasia	1931	Ithaca Reservoir Lake Ontario	Release with fish
Oncorhynchus kisutch	Coho salmon	Pacific	1933	Lake Erie	Deliberate release
Misgurnus anguillicaudatus	Oriental weatherfish	Asia	1939	Shiawassee River	Unintentional release
Morone americana[b]	White perch	Atlantic	1946	Lake Ontario	Canals
Phenacobius mirabilis	Suckermouth minnow	Mississippi	1950	Ohio	Canals, release with fish
Oncorhynchus nerka	Kokanee	Pacific	1950	Lake Ontario	Deliberate release
Oncorhynchus gorbuscha	Pink salmon	Pacific	1956	Current River	Unintentional release
Lepisosteus platostomus[a]	Shortnose gar	Mississippi	1962	Lake Winnebago	Canals
Ictiobus bubalus[a]	Smallmouth buffalo	Mississippi	1965	Big Lake	Deliberate release
~~*Notropis buchanani*~~	~~Ghost shiner~~	~~Mississippi~~	~~1979~~	~~Thames River~~	~~Release with fish~~
Alosa aestivalis[a]	Blueback herring	Atlantic	1981	Oneida Lake	Deliberate release, canals
Esox niger[a]	Chain pickerel	Atlantic	1985	Lake Erie	Deliberate release
Apeltes quadracus	Fourspine stickleback	Atlantic	1986	Thunder Bay	Shipping ballast water
Gymnocephalus cernua[b]	Eurasian ruffe	Eurasia	1986	St. Louis River	Shipping ballast water
Neogobius melanostomus	Round goby	Eurasia	1990	St. Clair River	Shipping ballast water
Proterorhinus semilunaris[b]	Tubenose goby	Eurasia	1990	St. Clair River	Shipping ballast water

[a] New addition.
[b] Information updated. Strike-through text indicates species that have been removed.

Petromyzon marinus (sea lamprey, Petromyzontidae) - revised introduction

While it has sometimes been argued that *P. marinus* may be native to Lake Ontario (Lawrie, 1970; Smith, 1985), Eshenroder (2014) makes a convincing argument that *P. marinus* first entered Lake Ontario during a watershed breach between the Susquehanna River (in which lamprey are native) and Lake Ontario in 1863. In 1863, a tributary of the Susquehanna River was diverted into the Oneida Lake drainage, and during this period water from the Susquehanna River drainage would have been sluiced directly into the Erie Canal. Sea lampreys entering the canal with this water would have reached the Seneca River, which flowed into the Oswego River, and proceeded from there into Lake Ontario. Earlier dates for *P. marinus* in Lake Ontario (1830s) as originally included in Mills have not been confirmed.

Alosa pseudoharengus (alewife, Clupeidae) – revised introduction

A. pseudoharengus was discovered in Lake Ontario in 1873 (Smith, 1985) and this date was used by Mills. It has been argued that this species was native to Lake Ontario but was depressed by Atlantic salmon and lake trout until the decline of these species in the late 1800s (Smith, 1970). However, documentation of an earlier population of alewife in Oneida Lake in 1868 (Smith, 1985), used here as the earliest date for the basin, supports the argument that the species expanded through the Erie Canal into the Great Lakes basin from the Atlantic drainage (Emery, 1985). It remains possible that *A. pseudoharengus* was accidentally introduced to Lake Ontario along with stocked shad in 1870 (Emery, 1985).

Oncorhynchus tshawytscha (chinook salmon, Salmonidae) – revised introduction

Emery's (1985) review places the first date for stocking of *O. tshawytscha* slightly earlier than Mills date of 1873, with a stocking in Lake Huron in 1870.

Carassius auratus (goldfish, Cyprinidae) – revised introduction

Original introductions of goldfish into North America began as early as the late 1600s and by 1842 the species was established in ponds in New York and other nearby states (DeKay, 1842). The earliest confirmed record of goldfish in the Great Lakes basin is in Lake Huron around 1880 (Emery, 1985) whereas Mills reported an introduction date of prior to 1878.

Cyprinus carpio (common carp, Cyprinidae) – revised introduction

The common carp (*C. carpio*) was first stocked into the Great Lakes basin in 1880 in Lake Huron after the U.S. Fish Commission distributed fish to Great Lakes states (reported in Mills as 'after 1879').

Pylodictis olivaris (flathead catfish, Ictaluridae) – added

Although early literature argued whether flathead catfish was native or introduced to the Great Lakes basin, and despite Hocutt and Wiley (1986) considering this species as likely native to Lake Erie, we conclude that the earliest records of this species in the basin following analysis of all available data are in Lake Erie 1890 at the mouth of the Huron River (Van Meter and Trautman, 1970) and Lake Michigan 1922 at the mouth of the Kalamazoo

River (Hubbs and Greene, 1926), which better match the sudden appearance and anomalously disjunct pattern typical of nonindigenous species. Fuller and Whelan (2018) provide a detailed review of the historical literature and data for this species.

Osmerus mordax (rainbow smelt, Osmeridae) – revised introduction

The earliest known record of rainbow smelt in the Great Lakes basin is a stocking in the St. Marys River in 1906 (Gerking, 1945). The species was also stocked in Crystal Lake, Michigan in 1912, which is in the Lake Michigan drainage (Van Oosten, 1937). Mills considered the planting in Crystal Lake to be the source for the upper Great Lakes populations of rainbow smelt rather than the earlier St. Marys River stocking. The origin of Lake Ontario populations has been debated. These populations are thought to have either been native to the lake or to have migrated up the Erie Canal system from the Atlantic drainage with an earliest report for Lake Ontario in 1947 (Smith, 1985). However, DeKay (1842) only noted rainbow smelt from coastal areas and did not record it from the upper Hudson River. At the time, the species was economically valuable in coastal markets. This coastal distribution suggests that rainbow smelt populations in the Lake Ontario basin in central New York are either not native or that they were overlooked in early surveys.

Enneacanthus gloriosus (bluespotted sunfish, Centrarchidae) – revised introduction

We significantly revise the estimated date for introduction of bluespotted sunfish to 1916 in Oneida Lake, New York (Smith, 1985). Although they have not been found in Oneida Lake again, this population may have spread by canal through the region and been the foundation for the population widespread in Lake Ontario tributaries by 1986. Alternatively, the Oneida Lake population may have died out without spreading; and the species subsequently reintroduced to Jamesville Reservoir, where it was found in 1971 (the date used by Mills), from an aquarium or bait bucket release.

Gambusia affinis (western mosquitofish, Poeciliidae) – taxonomic note

Gambusia affinis has been split into two species, *Gambusia affinis* and *Gambusia holbrooki*. For a brief period, GLANSIS listed both species. *Gambusia holbrooki* was recorded in the Great Lakes basin (Lower Maumee, OH) in 1947, but was extirpated in that location in 1948. Hubbs and Lagler (1958) reported that intergrades between *G. affinis* and *G. holbrooki* have been introduced into southern Michigan, but the stock did not become established. Other reports of introductions of *Gambusia* to the Great Lakes region appear consistent with the populations being *Gambusia affinis*.

Noturus insignis (margined madtom, Ictaluridae) – removed, native

Following Smith (1985), the native range of margined madtom is now considered to include the Black River watershed which drains into Lake Ontario at the headwaters of the St. Lawrence River. Thus we remove it from the list, as it is native to the basin. Nonetheless, this species has continued to expand its range within Lake Ontario and into the upper lakes.

Scardinius erythrophthalmus (rudd, Cyprinidae) – revised introduction

We revise the estimated date for introduction of rudd (*S. erythopthalmus*) to the Great Lakes basin to be significantly earlier than Mills report of the species in Lake Ontario in 1989 with a series of introductions of the species into the Finger Lakes region of New York beginning in the 1930s. These early introductions are believed by some to have failed and not to be the source of populations reported in widespread locations beginning in 1988 (Lake Winnebago, St. Lawrence River, Lake Ontario, Finger Lakes) which are instead attributed to use of *S. erythopthalmus* as bait (Burkhead and Williams, 1991). Nevertheless, we record the introduction date of 1931 as the most plausible earliest date of introduction.

Morone americana (white perch, Percichthyidae) – revised introduction

We revise the estimated date for introduction of white perch to the Great Lakes basin earlier to 1946 in Lake Ontario based on the review by Johnson and Evans (1990) instead of 1950 as used by Mills.

Phenacobius mirabilis (suckermouth minnow, Cyprinidae) – note on nativity

It is not certain if the records of this species from Michigan and parts of Ohio represent anthropogenic introductions or were simply the result of natural dispersal. In their summary table on fishes of the Central Appalachians and Central Atlantic Coastal Plain, Hocutt et al. (1986) listed *P. mirabilis* as native to the Muskingum drainage and noted the species may be native to a large part of Ohio. However, Trautman (1981) stated that the population in Buckeye Lake, Ohio, "possibly had been introduced inadvertently from the bait buckets of fishermen" and the species is listed as non-native to the Lake Erie basin in Van Meter and Trautman (1970). In their summary table on fishes of the Great Lakes basin, Bailey and Smith (1981) indicated that *P. mirabilis* had colonized tributaries of Lake Erie recently via canal or by natural dispersal. Similarly, O'Donnel (1935) found this species to be native to large parts of Illinois, but 'not present in the upland glacial lakes'. The suckermouth minnow did not occur in Michigan before the early 1900s (Latta et al., 2008). Natural eastward dispersal of the species has been rapid, and has occurred as a result of increased water turbidity and siltation following conversion of the prairies to farming. In the list of Michigan fishes given by Bailey and Smith (1992), *P. mirabilis* was denoted as one of several fishes "established through the direct or indirect intervention of humans". More recent surveys all list the species as non-native (Cudmore-Vokey and Crossman, 2000; McCrimmon Jr., 2002; Roth et al., 2013). We conclude this species does meet our criteria for nonindigenous in that (1) it appeared suddenly, (2) the distribution within the basin is restricted compared with native species, and (3) it has subsequently spread within the basin.

Lepisoteus platostomus (shortnose gar, Lepisosteidae) - added

Native to the Mississippi River, shortnose gar was first reported in the Great Lakes basin in Lake Winnebago in 1962 and presumed to have entered the lake through the canal at Portage into the Fox River; however, this introduction was believed to have failed. Becker (1983) reports the species as established in the Wolf River drainage, Fox River and lower Green Bay and to have entered the region through the Wisconsin-Fox Canal.

Ictiobus bubalus (smallmouth buffalo, Catostomidae) - added

Page and Burr (1991) consider smallmouth buffalo native to the Mississippi River basin and possibly to portions of the Lake Michigan drainage, but the species has not historically been collected below the ordinary high water mark of Lake Michigan. Populations established in Lake Erie are almost certainly the result of documented stocking events of the early 1900s (Leach, 1921, 1923).

Notropis buchanani (ghost shiner, Cyprinidae) - removed, native

Mills listed ghost shiner as nonindigenous to the Great Lakes based largely on evidence from Holm and Coker (1981) indicating that the population established in the Thames River in Kent County, Ontario (tributary to Lake St. Clair) first appeared in 1979 and was disjunct from native populations in the Mississippi

River basin. However, more recent analyses provide evidence that the species is native to Canadian portions of the Great Lakes basin (Kott and Fitzgerald, 2000; Holm et al., 2009; Roth et al., 2013; Reid et al., 2016; and Pers. Com.. N. Mandrak, 2019).

Alosa aestivalis (blueback herring, Clupeidae) - added

Juvenile *A. aestivalis* were collected in Oneida Lake in 1981 but mistakenly identified as juvenile *A. pseudoharengus* until the collection was reexamined in 1994, when an adult was collected (Pers. Com., Owens. 1994). Additional specimens were found in the Oswego River in 1994 and in Lake Ontario in 1995. Given the pattern of spread, the introduction was assumed to have been from the Hudson River, then traveling through the Mohawk (Greeley, 1935) and entered Oneida Lake via the Erie Barge Canal.

Esox niger (chain pickerel, Esocidae) - added

This species was first reported for the Great Lakes as a population in Lake Erie in Smith (1985) and attributed to stocking of the species as a sportfish. Chain pickerel has spread into both Lakes Ontario and Lake Huron.

Gymnocephalus cernua (ruffe, Percidae) – taxonomic revision

Note that the scientific name of this species was revised from *G. cernuus* back to *G. cernua*.

Proterorhinus semilunaris (tubenose goby, Gobiidae) – taxonomic revision

The scientific name of this species has changed from *P. marmoratus* to *P. semilunaris*. All tube-nosed gobies were previously included in a single species, *P. marmoratus*, which is now used only for the marine/brackish populations of the Black Sea while *P. semilunaris* is assigned to the freshwater species which has invaded the Great Lakes and other parts of Europe (Stepien and Tumeo, 2006).

Mollusks

There are now 18 species of nonindigenous mollusks established in the Great Lakes. Mills listed 14 species of mollusks as nonindigenous to the Great Lakes, including one unknown species that has since been identified as *Dreissena rostriformis bugensis*. Four species of mollusks have been added to the list (*Potamopyrgus antipodarum*, *Pisidium henslowanum*, *Pisidium moitessierianum*, and *Pisidium supinum*). First sightings have been revised for several species (Table 2). Below, we provide changes since Mills in information on previous introductions and the new nonindigenous species. We present this in chronological order by genus; if a species is not highlighted then there are no updates.

Elimia virginica (Piedmont elimia, Pleuroceridae) – revised common name

We note that the common name 'Piedmont elimia' has come into use for this species.

Pisidium spp. (Sphaeriidae) – 3 new species added

We add 3 species to the list of nonindigenous peaclams found in the Great Lakes basin in addition to *P. amnicum* which was listed by Mills. Despite the later date associated with *P. supinum*, Grigorovich et al. (2000) attributes the introduction of all 4 species to solid ballast.

Pisidium moitessierianum (pygmy peaclam) - added

Introduction of the pygmy peaclam pre-dates *P. amnicum* by 2 years with the first confirmed report of the species in 1895 in Lake Superior (EPA, 2008c). Early collections of this species were originally misidentified as *P. punctatum*.

Pisidium henslowanum (Henslow peaclam) - added

The first record of the Henslow peaclam for the Great Lakes basin is Lake Ontario in 1916, though the actual date of introduction may have been much earlier (Clarke, 1981).

Pisidium supinum (humpbacked peaclam) - added

The earliest confirmed record of the humpbacked peaclam in the Great Lakes basin was in Lake Ontario in 1959, though the actual date of introduction may have been much earlier (Clarke, 1981).

Table 2
Origin, date and location of first sighting, and vector(s) for nonindigenous aquatic mollusks of the Great Lakes.

Species	Common name	Origin	Date	Location	Vector
Elimia virginica	Piedmont elimia	Atlantic	1860	Erie Canal	Canals
Bithynia tentaculata	Faucet snail	Eurasia	1871	Lake Michigan	Shipping solid ballast, deliberate release
Pisidium moitessierianum[a]	Pygmy peaclam	Eurasia	1895	Lake Superior	Shipping solid ballast
Valvata piscinalis	European valve snail	Eurasia	1897	Lake Ontario	Shipping solid ballast
Pisidium amnicum	Greater European pea clam	Eurasia	1897	Genesee River	Shipping solid ballast
Sphaerium corneum[b]	European fingernail clam	Eurasia	1900	Lake Erie/Ontario	Shipping solid ballast
Radix auricularia	European ear snail	Eurasia	1901	Chicago, IL Lincoln Park pond	Aquarium release, unintentional release
Viviparus georgianus	Banded mystery snail	Mississippi	<1906	Lake Michigan	Aquarium release
Gillia altilis[b]	Buffalo pebblesnail	Atlantic	1915	Oneida Lake	Canals
Pisidium henslowanum[a]	Henslow peaclam	Eurasia	1916	Lake Ontario	Shipping solid ballast
Cipangopaludina chinensis malleata	Chinese mystery snail	Asia	1931	Niagara River	Aquarium release
Cipangopaludina japonica	Japanese mystery snail	Asia	1940	Lake Erie	Deliberate release
Lasmigona subviridis	Green floater	Atlantic	<1959	Erie Canal	Canals
Pisidium supinum[a]	Humpbacked peaclam	Eurasia	1959	Lake Ontario	Shipping solid ballast
Corbicula fluminea	Asiatic clam	Asia	1980	Lake Erie	Unintentional release (aquaculture, aquarium, fish)
Dreissena polymorpha[b]	Zebra mussel	Eurasia	1986	Lake Erie	Shipping (ballast water)
Dreissena rostriformis bugensis[b]	Quagga mussel	Eurasia	1989	Lake Erie	Shipping (ballast water)
Potamopyrgus antipodarum[a]	New Zealand mudsnail	Eurasia	1991	Lake Ontario	Shipping ballast water, release with fish

[a] New addition.
[b] Information updated.

Sphaerium corneum (European fingernail clam, Sphaeriidae) – revised introduction, vector assigned

We revise the introduction date of the European fingernail clam significantly earlier than Herrington's (1962) report (cited by Mills) of the species in Rice Lake in 1952, based on the assessment of Mackie (1995) which places the species in Lakes Erie and Ontario by "at least 1900." This earlier date and location(s) makes it likely that the species arrived via solid ballast, as did other molluscan invaders of that era.

Gillia altilis (Buffalo pebblesnail, Hydrobiidae) – revised introduction

Mills assigned this species an introduction date of 1918. We use the earliest record (acknowledged by Mills) of Buffalo pebblesnail as 1915 from Oneida Lake, NY, even though later surveys did not record the species at that location.

Cipangopaludina spp. (Chinese/Japanese mystery snails, Viviparidae) – taxonomic note

Mills acknowledged debate regarding the taxonomy of two species of viviparid snails, *Cipangopaludina chinensis malleata* and *Cipangopaludina japonica*, which centers on whether they should be treated as separate species. Twenty-five years later, the taxonomic argument is still not resolved, and ITIS still lists both as valid species names. We continue to distinguish between the introduction records for the two snail types and treat them as separate species despite continuing questions about their taxonomy.

Dreissena polymorpha (zebra mussel, Dreissenidae) – revised introduction

Earliest record of zebra mussel has been back-dated 2 years to 1986 where it was confirmed that the mussels had been present on natural gas wellheads in Lake Erie off Point Pelee in 1986 (Carlton, 2008).

Dreissena rostriformis bugensis (quagga mussel, Dreissenidae) – revised taxonomy and introduction

Mills noted the presence of a "new introduced species of *Dreissena*" verified in collections from the Ontario basin in 1991. *Re*-examination of earlier zebra mussel collections pinpoints the first collection of this species (identified as *D. rostriformis bugensis*) to 1989 in Lake Erie (Mills et al., 1993b). Like zebra mussels, the introduction of the quagga mussel is attributed to ballast water.

Potamopyrgus antipodarum (New Zealand mudsnail, Hydrobiidae) - added

The earliest record of New Zealand mudsnails in the Great Lakes basin are from Lake Ontario in 1991, with the original introduction attributed either to ballast water or to transfer with baitfish from the western states where they had been found as early as 1987 (Zaranko et al., 1997). This species made a jump to Lake Superior in 2001 (Grigorovich et al., 2003b) and spread to Lakes Michigan and Erie by 2006 (Levri et al., 2007).

Crustaceans

The list of crustaceans (Table 3) has grown considerably from the six originally listed by Mills; there are now 24 species of crustaceans nonindigenous to the Great Lakes. We remove *Gammarus fasciatus* from the list as more recent literature considers it to be a native which is expanding its range. We add 19 species to this list (*Cercopagis pengoi*, *Daphnia galeata galeata*, *Daphnia lumholtzi*, *Eubosmina maritima*, *Cyclops strenuus*, *Heteropsyllus nr. nunni*, *Megacyclops viridis*, *Neoergasilus japonicus*, *Nitokra hibernica*, *Nitokra incerta*, *Salmincola lotae*, *Schizopera borutzkyi*, *Echinogammarus ischnus*, *Gammarus tigrinus*, *Procambarus clarkia*, *Hemimysis anomala*, *Thermocyclops crassus*, *Diaphanosoma fluviatile*, and *Mesocyclops pehpeiensis*). Several of these represent older introductions that were 'missed' by Mills' analysis, but most represent more recent invasions. Below, we provide changes since Mills information on previous introductions and the new nonindigenous species. We present this in chronological order; if a species is not highlighted then there are no updates.

Gammarus fasciatus (Amphipoda) – removed, native

Although earlier records of *Gammarus fasciatus* predate 1940 (Hubricht and Mackin, 1940) and despite widespread distribution (Bousfield, 1958), based on the disjunct distribution (Chase Jr. et al., 1959), Mills concluded that the species was 'probably introduced' while noting that the natural distribution cannot be determined. However, Grigorovich et al. (2003a, 2003b) referred to new populations in Lake Superior as 'range expansions' and van Overdijk et al. (2003) referred to Lake Erie populations as native. We remove *Gammarus fasciatus* from our core list as an established nonindigenous species, and instead list it as a cryptogenic range expander.

Salmincola lotae (Copepoda) - added

Parasitic *S. lotae* was recorded from the Apostle Islands region of Lake Superior in 1985 in burbot (*Lota lota*) (Lasee et al., 1988). A review of the literature (Muzzall and Whelan, 2011) reveals one earlier report of this species in Lake Michigan in 1964. Notably, this earlier record was from *Coregonus hoyi*, which is not the usual host for *S. lotae*.

Bosmina coregoni (Cladocera) – revised taxonomy

Although the Integrated Taxonomic Information System still lists this species as *Eubosmina*, several sources (WoRMS, 2017; Haney et al., 2013) indicate that "*Eubosmina* as a genus is being eliminated from the literature in favor of *Bosmina*".

Procambarus clarkii (Decapoda) - added

The earliest confirmed report of *P. clarkii* in the Great Lakes system is from Sandusky Bay in 1967. Additional sporadic reports throughout the 1970s and 80s indicate this species has likely been established in this local area for a significant time. The species appears not to have expanded beyond this local population until recently, when reports attributed to organisms originating in the live food, classroom supply, and aquarium trade were reported elsewhere in the Great Lakes basin (starting around 2013).

Cyclops strenuus (Copepoda) - added

C. strenuous has been recorded from Lake Superior (1972) and a tributary to Lake Huron, St. Marys River (Selgeby, 1975; Reed and McIntyre, 1995; Hudson et al., 1998). *Cyclops strenuus* could have been introduced in ballast water, transferred with stocking programs, released with bait, discharged from live well water, transferred with recreational gear, transferred with waterfowl, or it may have dispersed via the Long Lac-Ogoki diversion project that connects the Hudson's Bay drainage to Lake Superior (Hudson et al., 1998; Grigorovich et al., 2003a, 2003b; Holeck et al., 2004; Duggan et al., 2005).

Nitokra hibernica (Copepoda) - added

N. hibernica was recorded for the first time from the mouth of the Niagara River on Lake Ontario in1972 and subsequently in southwestern Lake Ontario in 1973. It has also been recorded from Lake Michigan, Lake Erie, and Lake Huron (Czaika, 1978; Hudson et al., 1998; Lesko et al., 2003; Garza and Whitman, 2004). *Nitokra hibernica* was probably introduced in ballast water in ships entering the Great Lakes (Duggan et al., 2005).

Table 3
Origin, date and location of first sighting, and vector(s) for nonindigenous aquatic crustaceans of the Great Lakes.

Species	Common name	Origin	Date	Location	Vector
~~*Gammarus fasciatus*~~	~~Gammarid amphipod~~	~~Atlantic~~	~~<1940~~	~~Unknown~~	~~Shipping solid ballast, shipping ballast water~~
Eurytemora affinis	Calanoid copepod	widespread	1958	Lake Ontario	Shipping ballast water
Salmincola lotae[a]	Parasitic copepod	Eurasia	1964	Lake Michigan	Unknown
~~*Eubosmina*~~ *Bosmina coregoni*[b]	Water flea	Eurasia	1966	Lake Michigan	Shipping ballast water
Skistodiaptomus pallidus	Calanoid copepod	Mississippi	1967	Lake Ontario	Unintentional release, release with fish
Procambarus clarkii[a]	Red swamp crayfish	Gulf	1967	Sandusky Bay	Aquarium release
Cyclops strenuus[a]	Copepod	Circumboreal	1972	Lake Superior	Canals, shipping ballast water, release with fish
Nitokra hibernica[a]	Harpacticoid copepod	Eurasia	1972	Niagara River	Shipping ballast water
Daphnia galeata[a]	Waterflea	Eurasia	1980	Lake Erie	Shipping ballast water
Bythotrephes longimanus[b]	Spiny water flea	Eurasia	1982	Lake Ontario	Shipping ballast water
Eubosmina maritima[a]	Cladoceran	Eurasia	1988	Lake Michigan	Shipping ballast water
Gammarus tigrinus[a]	Amphipod	Atlantic	1985	Lake Superior	Shipping ballast water
Schizopera borutzkyi[a]	Oarsman	Europe	1988	Lake Michigan	Shipping ballast water
Argulus japonicus[b]	Parasitic copepod	Asia	1989	Lake Michigan	Aquarium release, release with fish
Megacyclops viridis[a]	Cyclopoid copepod	Europe	1994	Lake Superior	Shipping ballast water
Neoergasilus japonicus[a]	Parasitic copepod	Asia	1994	Lake Huron	Shipping ballast water, aquarium release, release with fish
Echinogammarus ischnus[a]	Scud	Europe	1994	Lake Erie	Shipping ballast water
Heteropsyllus nr. nunni[a]	Harpacticoid copepod	Atlantic?	1996	Lake Michigan	Shipping ballast water
Cercopagis pengoi[a]	Fishhook waterflea	Eurasia	1998	Lake Ontario	Shipping ballast water
Nitokra incerta[a]	Harpacticoid copepod	Eurasia	1999	Lake Erie	Shipping ballast water
Daphnia lumholtzi[a]	Waterflea	Australasia	1999	Lake Erie	Release with fish
Hemimysis anomala[a]	Bloody red shrimp	Eurasia	2006	Lakes Erie, Ontario, Michigan	Shipping ballast water
Thermocyclops crassus[a]	Copepod	Eurasia	2014	Lake Erie	Unknown
Diaphanosoma fluviatile[a]	Copepod	South America	2015	Lake Erie	Unintentional release
Mesocylops pehpeiensis[a]	Copepod	Asia	2016	Lake Erie	Unknown

[a] New addition.
[b] Information updated. Strike-through text indicates species that have been removed.

Daphnia galeata galeata (Cladocera) - added

Daphnia galeata was first divided into New World and European subspecies in 1957, though this division was not widely accepted until confirmed by modern genetic analyses. Taylor and Hebert (1993) show evidence of recent local hybridization of the North American native *Daphnia galeata mendotae* with the European *Daphnia galeata galeata* in populations of Lake Erie and Ontario watersheds (but not in the other 60 North American populations sampled). Patterns are consistent with a single introduction of *Daphnia galeata galeata* to Lake Erie via ballast water in the early 1980s. Their results demonstrate evidence for a significant 'hybrid advantage' within these local populations, where hybrids composed 90–100% of individuals. Despite hybridization, their work also showed that the two subspecies do not interbreed freely and suggest each should be accorded species status.

Bythotrephes longimanus (Cladocera) – revised taxonomy and introduction

Bythotrephes longimanus populations in the Great Lakes were originally identified as *Bythotrephes cederstroemi*, but 'recent work has shown that the taxon is conspecific to *B. longimanus*' (Berg et al., 2002). Earliest record of this species has been backdated two years to 1982 based on a report in Lake Ontario (Johannsson et al., 1991)

Eubosmina maritima (Cladocera) - added

This species was first collected in the Great Lakes region in August of 1988 in Green Bay (Lake Michigan). An abundant species in its native Baltic Sea, it has undergone several taxonomic revisions, most recently raised from variety (*Eubosmina longispina* forma *obtusirotris*) to species rank, which delayed its identification as an invader (De Melo and Hebert, 1994). *Eubosmina maritima* was very likely introduced in ballast water by ships entering the Great Lakes from Europe (De Melo and Hebert, 1994; Duggan et al., 2005).

Gammarus tigrinus (Amphipoda) - added

G. tigrinus was first discovered in Saginaw Bay, Lake Huron, in 2002. Archived material indicates that this species was present in Lake Superior and Lake Erie in 2001. Subsequent collections revealed that it is present in all of the Great Lakes (Grigorovich et al., 2005; Kelly et al., 2006). The earliest confirmed record of this species in the Great Lakes is from Duluth-Superior Harbor in 1985 (Trebitz et al., 2010). Very likely introduced in ballast water (Grigorovich et al., 2005), though populations of *G. tigrinus* in the Great Lakes are genetically similar to those from the Hudson River estuary (Kelly et al., 2006).

Schizopera borutzkyi (Copepoda) - added

Schizopera borutzkyi was recorded for the first time in Lake Michigan in 1988 (Horvath et al., 2001). Its continued presence in the lake was confirmed in subsequent years (Garza and Whitman, 2004). It was discovered in Lake Erie in 2003 (Lesko et al., 2003).

Argulus japonicus (Copepoda) – revised introduction

The earliest confirmed date for collection of *A. japonicus* in the Great Lakes is revised from 1988 to to 1989 per LaMarre and Cochran (1992). This species may have been widespread in the Great Lakes well before this date. This parasite is a generalist, demonstrating little host specificity.

Megacyclops viridis (Copepoda) - added

Megacyclops viridis was first reported in 1994 in Duluth Harbor, Lake Superior (Ogle et al., 1995). It has also been reported in the River Canard (south of Windsor, Ontario in the Detroit River drainage) in 1998 (Hudson et al., 1998). *Megacyclops viridis* was very likely introduced in ballast water in ships entering the Great Lakes (Hudson et al., 1998).

Neoergasilus japonicus (Copepoda) - added

The parasitic copepod *N. japonicus* was first reported in 1994 in the Great Lakes basin in Saginaw Bay, Lake Huron (Hudson and Bowen II, 2002) in four species of fish (*Pimephales promelas*, *Micropterus salmoides*, *Lepomis gibbosus*, and *Perca flavescens*). Further sampling found the parasite in seven additional species (*Lepomis macrochirus*, *Cyprinus carpio*, *Ictalurus punctatus*, *Carassius auratus*, *Lepomis cyanellus*, *Ambloplites rupestris*, and *Micropterus dolomieu*). It is most likely that the introduction was associated with fish culture, but it could have occurred via the aquarium trade, aquaculture, bait release, or ballast water introduction (Hudson and Bowen II, 2002).

Echinogammarus ischnus (Amphipoda) - added

E. ischnus was first reported in 1994 from the Detroit River (Witt et al., 1997). Archived specimens show that it could have been present in western Lake Erie as early as 1993 (van Overdijk et al., 2003). The species is now widespread in the Great Lakes. *Echinogammarus ischnus* was almost certainly introduced in ballast water (Witt et al., 1997).

Heteropsyllus nr. nunni (Copepoda) - added

This species was recorded for the first time in 1996 from Lake Michigan. A few individuals have also been recorded from Lake St. Clair (Horvath et al., 2001) and northwestern Lake Huron. Probably introduced in ballast water, like most other copepod species introduced to the Great Lakes (Horvath et al., 2001).

Cercopagis pengoi (Cladocera) - added

The fishhook water flea (*C. pengoi*) was first discovered during EPA monitoring cruises on Lake Ontario in 1998 (EPA, 2008a). It rapidly spread throughout Lake Ontario and into Lake Michigan and the Finger Lakes. This species is believed to have entered the Great Lakes via ballast water, but spread rapidly through fouling of recreational vessels and gear.

Nitokra incerta (Copepoda) - added

N. incerta was reported for the first time in 1999 from the Detroit River where it joins Lake Erie (Grigorovich et al., 2001). The species probably arrived in the ballast water of overseas shipping. Duggan et al. (2005) found other *Nitokra* spp. in ballast water of ships entering the Great Lakes, although *N. incerta* was not present.

Daphnia lumholtzi (Cladocera) - added

A native of tropical and subtropical lakes in east Africa, Australia and India, *D. lumholtzi* likely was introduced to the southern U.S. with shipments of Nile Perch and has spread via contaminated fish stocks, baitfish and with recreational boats (Havel and Hebert, 1993). This species was reported just south of the Great Lakes basin in Grand Lake St. Mary's in 1993 and had reached Lake Erie by 1999 (Muzinic, 2000). Although subtropical and not well-adapted to the Great Lakes climate, ephippia of *D. lumholtzi* have proven capable of overwintering.

Hemimysis anomala (Mysid) - added

H. anomala was reported for the first time in 2006 from two disjunct regions in the Great Lakes: southeastern Lake Ontario at Nine Mile Point near Oswego, New York, in May 2006 (Pers. Com. J. Wyda 2007); and from a channel connecting Muskegon Lake to Lake Michigan in November 2006 (Pothoven et al., 2007). The presence of disjunct populations suggests that this species may have entered the Great Lakes significantly earlier. *Hemimysis anomala* is native to freshwater margins of the Black Sea, the Azov Sea and the eastern Ponto-Caspian Sea. It has historically occurred in the lower reaches of the Don, Danube, Dnieper and Dniester rivers. Like other Ponto-Caspian species, we assign it as likely to have been introduced with ballast water.

Thermocyclops crassus (Copepoda) - added

This species was reported by US EPA in 2016 after specimens were verified in samples from Lake Erie in 2014, 2015 and 2016 (Connolly et al., 2017). *T. crassus* was reported in Lake Champlain in 1991 (Duchovnay et al., 1992); it is uncertain whether the population in Lake Erie represents a spread from the Lake Champlain population or perhaps predated it but remained undetected due to similarity with the native *Mesocyclops edax*. Note that Duggan et al. (2005) reported this species as present in a single ballast tank entering the Great Lakes (sampled 2001–2002), which would be a credible alternative introduction for the current established population. However, the authors explicitly state that the species 'does not have an established population in the Great Lakes' at that time and that probability of successful establishment may be constrained by propagule supply.

Diaphanosoma fluviatile (Copepoda) – added

This species was reported by USEPA and Cornell in 2018 after specimens were verified in samples taken from Lake Erie in 2015. Overwintering and reproduction of this species were confirmed in early 2019 as well as its spread to Lake Michigan and Lake Superior. This species is considered established in the southern US (earliest US report Florida, 1960 – Korovchinsky, 2002) and most likely arrived in the Great Lakes as a hitchhiker with recreational boats, gear, bait or ornamentals from the southern populations.

Mesocyclops pehpeiensis (Copepoda) - added

This species was reported by USEPA and Cornell in 2018 after specimens were verified in samples taken from Lake Erie in 2016 and 2017. *Mesocyclops pehpeiensis* was previously established in the southern US (Reid, 1993) and has a history of transfer with ornamental plants and aquaculture.

Other invertebrates

There are a total of 19 'other' nonindigenous invertebrates (i.e., non-mollusk, non-crustacean) in the Great Lakes (Table 4). We have added 11 nonindigenous species (*Potamothrix bedoti*, *P. moldaviensis*, *P. vejdovskyi*, *Schyzocotyle acheilognathi*, *Dactylogyrus amphibothrium*, *D. hemiamphibothrium*, *Ichthyocotylurus pileatus*, *Neascus brevicaudatus*, *Scolex pleuronectis*, *Timoniella* sp., and *Lophopodella carteri*) to the eight species originally listed by Mills.

Ichthyocotylurus pileatus (Platyhelminthes) - added

Ichthyocotylurus pileatus, a digenean fluke, was first reported in 1929 in trout perch (*Percopsis omiscomaycus*) in Lake Erie (Bangham and Hunter, 1939). It has also been found in yellow perch (*Perca flavescens*), walleye (*Stizostedion vitreum*), round goby (*Neogobius melanostomus*) and Eurasian ruffe (*Gymnocephalus cernua*). The parasite is believed to be native to the Ponto-Caspian and to have entered the lakes with a host fish.

Lophopodella carteri (Bryozoa) - added

L. carteri, a bryozoan native to Southeast Asia, was first reported in the Lake Erie basin in 1934 (Grigorovich et al., 2003a, 2003b). In

Table 4
Origin, date and location of first sighting, and vector(s) for other nonindigenous aquatic invertebrates of the Great Lakes.

Species	Common name	Origin	Date	Location	Vector
Ichthyocotylurus pileatus[a]	Digenean fluke	Eurasia	1929	Lake Erie	Release with fish
Craspedacusta sowerbyi	Freshwater jellyfish	Asia	1933	Lake Erie	Unintentional release
Lophopodella carteri[a]	Freshwater bryozoan	Asia	1934	Lake Erie	Release with plants
Tanysphyrus lemnae[b]	Aquatic weevil	Eurasia	1934	Cayuga Lake	Unknown
Acentria ephemerella[b]	Aquatic moth	Eurasia	1938	Oswego River	Unintentional release
Branchiura sowerbyi	Tubificid worm	Asia	1951	Kalamazoo River	Unintentional release
Potamothrix moldaviensis[a]	Tubificid worm	Eurasia	1952	Lake Ontario	Shipping ballast water
Cordylophora caspia	Hydroid	Unknown	1956	Lake Erie	Unintentional release
Potamothrix vejdovskyi[a]	Tubificid worm	Eurasia	1965	Lake Erie	Shipping ballast water
Dugesia polychroa	Flatworm	Eurasia	1968	Lake Ontario	Shipping ballast water
Potamothrix bedoti[a]	Tubificid worm	Eurasia	1975	Lake Michigan	Shipping ballast water
Ripistes parasita	Tubificid worm	Eurasia	1980	North Channel	Shipping ballast water
Gianius aquaedulcis[b]	Tubificid worm	Eurasia	1983	Niagara River	Shipping ballast water
Dactylogyrus amphibothrium[a]	Monogenetic fluke	Eurasia	1992	Lake Superior	Release with fish, shipping ballast water
Dactylogyrus hemiamphibothrium[a]	Monogenetic fluke	Eurasia	1992	Lake Superior	Release with fish, shipping ballast water
Neascus brevicaudatus[a]	Dignean fluke, trematode	Eurasia	1992	St. Louis River	Release with fish, shipping ballast water
Timoniella sp.[a]	Dignean fluke, trematode	Eurasia	1992	Lake Superior	Release with fish, shipping ballast water
Scolex pleuronectis[a]	Cestode	Eurasia	1994	Lake St. Clair	Release with fish, shipping ballast water
Schyzocotyle acheilognathi[a]	Asian tapeworm	Asia	2001	Peter Lake	Release with fish

[a] New addition.
[b] Information updated.

more recent years, it has spread to Lake Michigan (Lauer et al., 1999) and inland lakes in the region. This species likely entered the Great Lakes as a contaminant with aquatic plants.

Tanysphyrus lemnae (Insecta) – revised introduction

The earliest record of *T. lemnae* in the Great Lakes basin is backdated by nearly a decade to a report in Cayuga Lake, NY in 1934 (Scotland, 1934).

Acentria ephemerella (Insecta) – revised taxonomy and introduction

In the Integrated Taxonomic Information System (ITIS, 2018), *Acentropus niveus* and *A. ephemerella* are both listed as valid but unverified species names (citing 1996 Code). Bernd Blossey (Cornell U., Pers. Com. 2012) advised that *Acentria ephemerella* is the correct, valid name per Passoa (1988). The earliest report of this species is backdated more than a decade to 1938 with a report for the Oswego River near Lake Ontario (Forbes, 1938).

The European *Acentropus niveus* was first collected in North America in Montreal, Quebec, in 1927 (Sheppard, 1945). By 1950, the moth had been found in Lake Erie, Lake Ontario, and various locations within their drainage basins (Forbes, 1938; Judd, 1950).

Potamothrix spp. (Oligochaetes) – added 3 species

Three species of *Potamothrix* were added to the list based on the assessment of Grigorovich et al. (2003a, 2003b). The earliest record of *P. moldaviensis* is 1952 in Lake Ontario, of *P. vejdovskyi* is 1965 in Lake Erie, and of *P. bedoti* is 1975 in Lake Michigan. It is possible that all three species were introduced prior to 1959 and remained undetected due to difficulty of identification of this group to the species level.

Gianius aquaedulcis (Oligochaetes) - revised taxonomy

Gianius sp. was revised by Erseus (1992) to *Phallodrilinae*, splitting the genus into 20 different genera where *Phallodrilus aquaedulcis* became *Gianius aquaedulcis*.

Dactylogyrus spp. (Platyhelminthes) – Added 2 species.

The US Department of Interior (1993) reported 2 species of *Dactylogyrus* (*D. amphibothrium* and *D. hemiamphibothrium*) in Eurasian ruffe in Lake Superior in 1992. Although no earlier reports can be confirmed, these two species are presumed to have been introduced along with Eurasian ruffe (in 1986) as this is the sole known host.

Neascus brevicaudatus (Platyhelminthes) added

N. brevicaudatus is a fluke that attaches to the eyes of a host fish. This species was also reported by US Department of Interior (1993) in Eurasian ruffe taken from the St. Louis River (tributary to Lake Superior) in 1992. It is assumed to have been introduced along with Eurasian ruffe (in 1986) as all Great Lakes representatives of the species to date have been found in ruffe.

Timoniella sp. (Platyhelminthes) - added

Timoniella sp. was reported for the Great Lakes basin in Lake Superior with Eurasian ruffe in 1992 (Pronin et al., 1997). The parasite was not identified to the species level but was found at such sufficient densities that it was assumed to be established. It is assumed to have been introduced along with Eurasian ruffe (in 1986) as all Great Lakes representatives of the species to date have been found in ruffe.

Scolex pleuronectis (Platyhelminthes) - added

S. pleuronectis was first isolated in 1994 from round goby in the St. Clair River (Pronin et al., 1997). It is assumed to have entered the Great Lakes along with the round goby (in 1990), as this is a common parasite in round goby in the Black Sea (Pronin et al., 1997).

Schyzocotyle acheilognathi (Platyhelminthes) - added

This species was renamed from *Bothriocephalus acheilognathi* (Marcogliese et al., 2016). Two gravid *S. acheilognathi* were collected from a fathead minnow (*Pimephales promelas*) in Peter Lake, Michigan in 2001 (Choudhury et al., 2006). The parasite is likely to have been accidentally introduced with grass carp, one of its native hosts, and subsequently spread through the translocation of bait fish (Choudhury et al., 2006; Heckmann et al., 1993). Emerald shiners (*Notropis atherinoides*) were infected by this parasite in 2009–2010 at most localities, including from the St. Clair River, the Detroit River, Lake Erie, the Niagara River, and Lake Ontario (Marcogliese et al., 2016).

Microbes

There are now 15 known nonindigenous microbes in the Great Lakes (Table 5); a substantial increase from Mills' original three. We added 2 additional bacteria (*Piscirickettsia* cf. *salmonis* and *Renibacterium salmoninarum*), 4 additional protozoan parasites

Table 5
Origin, date and location of first sighting, and vector(s) for nonindigenous aquatic microbes of the Great Lakes.

Species	Common name	Origin	Date	Location	Vector
Aeromonas salmonicida[b]	Furunculosis	Unknown	1902	Unknown	Release with fish
Glugea hertwigi[b]	Microsporidian parasite	Eurasia	1918	Muskegon River watershed	Release with fish
Renibacterium (*Corynebacterium*) *salmoninarum*[a]	Bacterial kidney disease (BKD)	Europe	1967	Lake Michigan	Release with fish
Myxobolus cerebralis	Salmonid whirling disease	Europe	1968	Ohio	Release with fish
Trypanosoma acerinae[a]	Flagellated parasite	Eurasia	1992	St. Louis River	Release with fish, shipping ballast water
Sphaeromyxa sevastopoli[a]	Myxosporean parasite	Eurasia	1994	Lake St. Clair	Release with fish, shipping ballast water
Acineta nitocrae[a]	Suctorian ciliate	Eurasia	1997	Lake Erie	Shipping ballast water
Novirhabdovirus sp. *genotype IV sublineage b*[a]	Viral hemorrhagic septicemia (VHS)	Atlantic	1999	Lake Otario, Lake Erie, Lake St. Clair	Shipping ballast water, release with fish
Heterosporis sutherlandae[a]	Microsporidian parasite	Eurasia	2000	Lake Ontario	Shipping ballast water, release with fish, release aquarium
Ranavirus[a]	Largemouth bass virus (LMBV)	Asia	2000	Lake Ontario	Release with fish
Rhabdovirus carpio[a]	Spring viremia of carp (SVC)	Eurasia	2001	Lake Michigan	Release with fish
Piscirickettsia cf. *salmonis*[a]	Muskie pox	Unknown	2002	Lake St. Clair	Unknown
Psammonobiotus communis[a]	Testate amoeba	Eurasia	2002	widespread	Shipping ballast water
Psammonobiotus dzwinowi[a]	Testate amoeba	Eurasia	2002	widespread	Shipping ballast water
Psammonobiotus linearis[a]	Testate amoeba	Eurasia	2002	Lake Erie and Ontario	Shipping ballast water

[a] New addition.
[b] Information updated.

(*Acineta nitocrae*, *Heterosporis* sp., *Sphaeromyxa sevastopoli*, and *Trypanosoma acerinae*), 3 free-living protozoans (*Psammonobious* spp.), and 3 viruses (those responsible for viral hemorrhagic septicemia, largemouth bass virus and spring viremia of carp).

Aeromonas salmonicida (furunculosis, Bacteria) – vector assigned

Mills assigned this as vector unknown. We assume it entered the Great Lakes with a stocked host fish (Crawford, 2001) and so assign it the vector 'Release with Fish'.

Glugea hertwigi (Microsporidea) – revised introduction

The first confirmed report of this species noted by Mills was 1960 in Lake Erie. We found a significantly earlier report of the species in 1918 in inland waters near Cadillac, Michigan in the Lake Michigan watershed (Univ. of Michigan Herbarium). Given that its host, *Osmerus mordax*, was already established in the Lake Michigan watershed by this date, we find the report credible and note that it does not alter Mills' assertion that *G. hertwigi* invaded with *O. mordax*.

Renibacterium (Corynebacterium) salmoninarum (bacteria) - added

Bacteria kidney disease (BKD) was first reported in the Great Lakes in Lake Michigan in 1967 (Holey et al., 1998). The responsible bacteria is believed to have entered the Great Lakes with stocked chinook salmon (Bronte et al., 2003).

Trypanosoma acerinae (protozoan) - added

This blood parasite was first isolated in the Great Lakes from Eurasian ruffe in Pokegama Bay (St. Louis River, a Lake Superior tributary), Wisconsin in 1992 (Pronin et al., 1998). It was likely introduced with Eurasian ruffe (in 1986). A slightly earlier collection of *Trypanosoma* from Lake Michigan sculpins (*Cottus bairdii* and *Cottus cognatus*) in 1985 was not originally identified to species and may have been mistakenly presumed to have been *T. acerinae*.

Sphaeromyxa sevastopoli (protozoan) - added

S. sevastopoli was first discovered in the Great Lakes in the gall bladders of exotic gobies collected from the St. Clair River and Lake St. Clair in 1994 (Pronin et al., 1997). The parasite is believed to have been introduced with round gobies (in 1990) (Pronin et al., 1997; Rolbiecki, 2006).

Acineta nitocrae (protozoan) - added

This epizootic parasite of copepods was first reported in the Great Lakes from Lake Erie in 1997 on nonindigenous copepods of the Genus *Nitokra* (Grigorovich et al., 2001). It was likely introduced along with one of its hosts – *Nitokra hibernica* (first report 1972) or *N. incerta* (first report 1999) (Grigorovich et al., 2001).

Novirhabdovirus sp. genotype IV sublineage b (virus) - added

Reexamination of preserved specimens from fish kills has been able to confirm that the virus responsible for viral hemorrhagic septicemia (VHS) was already present in Lake Ontario and Lake St. Clair in 1999 (USDA, 2006). This virus is most closely related to a marine strain that originated on the east coast of North America (Elsayed et al., 2006). This suggests that it is possible the virus entered the Great Lakes either with migrating fish or in ballast water.

Heterosporis sutherlandae (protozoa) - added

Heterosporis (not identified to species) was first isolated in the Great Lakes basin from yellow perch in Catfish Lake, Wisconsin in 2000 and was found in eastern Lake Ontario later that same year (Sutherland, 2002; Sutherland et al., 2004). This parasite may have been introduced with the movement of water (e.g., live wells, bait buckets) or with a baitfish host or via infected aquarium water (Sutherland et al., 2000; Lom et al., 1989; Lom et al., 1993). In Europe and Asia it is reported for a wide diversity of host species including eels, angelfish, bettas, perch, cichlids, and catfish. Phelps et al. (2015) found it to be a novel species genetically distinct from the known Asian and European species that have been sequenced and designated it as *Heterosporis sutherlandae*.

Ranavirus (virus) - added

The largemouth bass virus (LMBV) was first detected within the Great Lakes basin in the Bay of Quinte, Lake Ontario in 2000 (Sutherland et al., 2004). This virus most likely entered the Great Lakes with infected fish or with water from live wells or bait buckets based on presence in southern US hatcheries slightly prior (1999) to detection in the Great Lakes and in wild populations in the southern US in the mid-1990s (Plumb et al., 1996).

Rhabdovirus carpio (virus) - added

Spring viremia of carp is a viral disease caused by *Rhabdovirus carpio*. The earliest confirmed report for the Great Lakes basin

was in Lake Michigan in 2001 in common carp (carriers, not a fish kill). The first reports of this species in the US were in koi, and it is believed the virus was introduced with water garden escapees (Goodwin, 2003).

Piscirickettsia cf. salmonis (bacteria) - added

P cf. *salmonis* was first detected in the Great Lakes from muskellunge (*Esox masquinongy*) in Lake St. Clair in May 2002 (Michigan DNR, 2002). The disease is called muskie pox in muskellunge and salmonid rickettsial septicemia in salmon. The bacteria was probably introduced with stocked salmonids, based on salmonids being the principal host and the presence of the microbe both Atlantic and Pacific North American salmonid populations prior to detection in the Great Lakes (Fryer and Hedrick, 2003).

Psammonobiotus spp. (protozoa) – added 3 species

Three species of nonindigenous testate amoebae were reported by Nicholls and MacIsaac (2004) in surveys undertaken in 2002. All three species are psammonobionts found attached to sand grains and may have been overlooked for a very long time prior to discovery. All three are native to the Ponto-Caspian region and previously reported in the Baltic Sea (Nicholls and MacIsaac, 2004) making it highly likely they entered the Great Lakes with ballast water. *P. communis* and *P. dzwinowi* are widespread, found in all the lakes sampled (Lake Michigan was not surveyed). *P. linearis* appears to be limited to the lower Great Lakes (Erie and Ontario).

Algae

Mills reported 24 species of algae as nonindigenous to the Great Lakes (Table 6). These species have undergone significant taxonomic revision. We add 3 species (*Ulva flexuosa*, *Thalassiosira baltica and Cylindrospermopsis raciborskii*) bringing the total to 27 nonindigenous species of algae.

Ulva (Enteromorpha) intestinalis & Ulva (Enteromorpha) prolifera (Chlorophyceae) – revised taxonomy

Although ITIS (2018) cites these two species as Genus *Enteromorpha* (as in Mills), the more recently updated AlgaeBase (2015) lists the preferred name for the entire genus as *Ulva* citing Hayden et al., 2003.

Stephanodiscus binderanus (Bacillariophyceae) – revised introduction

The first record of this species in the Great Lakes basin was listed by Mills as 1938 in Lake Michigan. Paleolimnological evidence revises the earliest record to Lake Erie to 1930 (Stoermer et al., 1996). A recent study conducted by Hawryshyn et al. (2012) found a historical microfossil presence of *S. binderanus* dating back to the 17th century in Lake Simcoe, Ontario. This discovery brings the status of *S. binderanus* as a nonindigenous species in the Great Lakes basin into question; however, similar records have not yet been found within the Great Lakes.

Discostella pseudostelligera (Bacillariophyceae) – revised taxonomy and introduction

Although ITIS (2018) cites *Cyclotella pseudostelligera* as the valid name for this species, the more recently updated AlgaeBase (2015) lists *Discostella pseudostelligera* as the currently accepted name (confirmed by taxonomic expert M. Guiry, Pers. Com. 2013) according to Houk and Klee (2004). Houk and Klee proposed the transfer of the stelligeroid taxa of the genus *Cyclotella* to the new genus *Discostella* because of differences in characteristics that include marginal fultoportulae and the rimoportuale positioned between costae. Mills lists the first record of this species as Lake

Table 6
Origin, date and location of first sighting, and vector(s) for nonindigenous aquatic algae of the Great Lakes.

Species	Common name	Origin	Date	Location	Vector
Ulva (*Enteromorpha*) *intestinalis*[b]	Green alga	Atlantic	1926	Wolf Creek (Ontario)	Unintentional release
Stephanodiscus binderanus[b]	Diatom	Eurasia	1930	Lake Erie	Shipping ballast water
Discostella pseudostelligera[b]	Diatom	Widespread	1935	Lake Michigan	Shipping ballast water
Diatoma ehrenbergii[b]	Diatom	Widespread	1938	Lake Michigan	Shipping ballast water
Actinocyclus normanii fo. subsalsa	Diatom	Eurasia	1938	Lake Ontario	Shipping ballast water
Bangia atropurpurea[b]	Red alga	Europe	1944	Lake Superior tributaries	Shipping ballast water or fouling
Stephanodiscus subtilis	Diatom	Eurasia	1946	Lake Michigan	Shipping ballast water
Thalassiosira weissflogii	Diatom	Widespread	1962	Detroit River	Shipping ballast water
Skeletonema potamos	Diatom	Widespread	1963	Toledo, Ohio	Shipping ballast water
Cyclotella atomus	Diatom	Widespread	1964	Lake Michigan	Shipping ballast water
Cyclotella cryptica	Diatom	Widespread	1964	Lake Michigan	Shipping ballast water
Discostella woltereki[b]	Diatom	Widespread	1964	Lake Michigan	Shipping ballast water
Chroodactylon ornatum[b]	Red alga	Atlantic	1964	Lake Erie	Shipping ballast water
Cylindrospermopsis raciborskii[a]	Cylindro	S. America	1971	Lake Erie	Shipping, recreational boating, or dispersal
Contricribra guillardii	Diatom	Widespread	1973	Sandusky Bay	Shipping ballast water
Thalassiosira pseudonana	Diatom	Widespread	1973	Lake Erie	Shipping ballast water
Skeletonema subsalsum	Diatom	Eurasia	1973	Sandusky Bay	Shipping ballast water
Hymenomonas roseola	Coccolithophorid	Eurasia	1975	Lake Huron	Shipping ballast water
Sphacelaria fluviatilis	Brown alga	Asia	1975	Gull Lake	Unintentional release, aquarium release
Sphacelaria lacustris	Brown alga	Unknown	1975	Lake Michigan	Shipping ballast water
Thalassiosira bramaputrae	Diatom	Widespread	<1978	Lake Erie	Shipping ballast water
Chaetoceros muelleri var subsalsum[b]	Diatom	Unknown	1978	Lake Huron	Shipping ballast water
Pleurosira laevis[b]	Diatom	Widespread	1978	Lake Michigan	Shipping ballast water
Nitellopsis obtusa	Starry stonewort	Eurasia	1978	St. Lawrence River	Shipping ballast water
Ulva (*Enteromorpha*) *prolifera*	Green alga	Atlantic	1979	Lake St. Clair	Unknown
Thalassiosira baltica[a]	Diatom	Baltic	1988	Lake Ontario	Shipping ballast water
Ulva (*Enteromorpha*) *flexuosa* subsp. *flexuosa* and subsp. *paradoxa*[a]	Green alga	Unknown	2003	Muskegon Lake (M)	Shipping ballast water

[a] New addition.
[b] Information updated.

Michigan in 1946, but we revise the date to 1935 based on Stoermer and Yang (1970).

Diatoma ehrenbergii (Bacillariophyceae) - revised introduction

Mills lists the first record of this species as Lake Michigan in the 1930s. We use the more specific date of 1938 per Stoermer and Yang (1970).

Bangia atropurpurea (Rhodophyceae) – revised introduction and taxonomic note

ITIS (2018) lists *Bangia atropurpurea* as an unaccepted name, with a correction of the name to *Bangia fusco-purpurea* citing NODC Taxonomic Code, database (version 8.0) 1996. We briefly changed the name of the species in the GLANSIS database to reflect ITIS. However, recent publications (Chou et al., 2015; Shea et al. Shea et al., 2014) verified by personal communications (K. Muller, 2015) indicate that this name change applied to only marine members of the species; freshwater strains were retained as *Bangia atropurpurea*. This reverses an earlier revision (1991) combining the marine and freshwater species into the single taxa (as *Bangia atropurpurea*).

Mills officially lists the first record of this species as 1964 in Lake Erie, while noting earlier records in tributaries in the 1940s. We use this earlier record (Smith Jr. and Moyle, 1944) to place the first report of the species in Lake Superior in 1944.

Discostella woltereki (Bacillariophyceae) – revised taxonomy

Although ITIS cites *Cyclotella woltereckii* as the valid name for this species, the more recently updated AlgaeBase (2015) lists *Discostella woltereckii* as the currently accepted name (confirmed by taxonomic expert M. Guiry, Pers. Com. 2013) according to Houk and Klee (2004). Houk and Klee proposed the transfer of the stelligeroid taxa of the genus *Cyclotella* to the new genus *Discostella* because of differences in characteristics that include marginal fultoportulae and the rimoportuale positioned between costae.

Chroodactylon ornatum (Rhodophyceae) – revised taxonomy

This species has been recorded under various names from freshwater and marine environments in Europe, North America, the Caribbean islands, the Pacific islands, the Atlantic islands, southern Asia, South America, Africa, the Indian Ocean islands, Australia, and New Zealand. Formerly, the genus name *Chroothece* also often referred to freshwater forms of this species. Originally, the species found in Lake Huron was identified as *Asterocystis smargdina*. This species is not included in ITIS (2018) under any known synonym; AlgaeBase (2015) lists *Chroodactylon ramosum* (as used by Mills) as a non-preferred synonym for *C. ornatum*, hence our shift to this nomenclature.

Cylindrospermopsis raciborskii (Nostocaceae) - added

C. raciborskii is a filamentous blue-green algae historically regarded as subtropical, but is expanding into temperate regions worldwide. The earliest record of the species in the Great Lakes is 1971 in Lake Erie (as a minor component of the assemblage), but in recent years the species has begun contributing to blooms in the drowned river mouth lakes (Mona Lake and Muskegon Lake) along Lake Michigan. The strain present in the Great Lakes is closely related to South American strains, indicating probable introduction via ballast, though movement with migrating waterfowl is also a possible vector (Hong et al., 2006).

Contricribra guillardii (Bacillariophyceae) – revised taxonomy

Although ITIS (2018) still cites *Thalassiosira guillardii* (as used by Mills) as the valid name for this species, the more recently updated AlgaeBase (2015) lists *Contricribra guillardii* as the currently accepted name citing Stachura-Suchoples and Williams (2009).

Thalassiosira bramaputrae – revised taxonomy

ITIS (2018) no longer lists *Thalassiosira lacustris* as a valid name; citing the revisions of Hakansson and Locker (1981), ITIS moves the Great Lakes species to *Thalassiosira bramaputrae*.

Chaetoceros muelleri var. subsalsum (Bacillariophyceae) – revised taxonomy

ITIS (2018) no longer lists *Chaetoceros hohnii* as a valid name; following the revisions of Johans and Rushforth the species found in the Great Lakes is now considered to be a subspecies of *Chaetoceros muelleri* var. *subsalsum* (Stoermer et al., 1999).

Pleurosira laevis (Bacillariophyceae) – revised taxonomy

ITIS (2018) no longer lists *Biddulphia laevis* as a valid species. The accepted name for the species found in the Great Lakes is now *Pleurosira laevis* (Stoermer et al., 1999).

Nitellopsis obtusa (Chlorophyceae) – revised introduction

The common name "starry stonewort" is now in widespread usage for this species in the Great Lakes basin. Mills places the first report of *N. obtusa* in Lake St. Clair in 1983; we revise this to 1978 for the St. Lawrence River based on Geis et al. (1981).

Thalassiosira baltica (Bacillariophyceae) - added

T. baltica joins 3 other *Thalassiosira* species that have invaded the Great Lakes from the Baltic via ballast water. The first confirmed report of this species comes from Lake Ontario in 1988 (Edlund et al., 2000).

Ulva (Enteromorpha) flexuosa subsp. flexuosa and subsp. paradoxa (Chlorophyceae) - added

Although ITIS (2018) cites this species as Genus *Enteromorpha*, the more recently updated AlgaeBase (2015) lists the preferred name for the entire genus as *Ulva*, citing Hayden et al., 2003. The first report of this species in the region is as a bloom in Muskegon Lake (connected to Lake Michigan) in 2003. This species prefers saline waters and may be restricted to areas with runoff of road salt. It is assumed this species reached the Great Lakes in ballast water or on ship hulls (Lougheed and Stevenson, 2004).

Plants

There are 58 nonindigenous aquatic plants in the Great Lakes basin- the same number as reported by Mills, though there have been four removals and four additions (Table 7). In adopting a definition for "aquatic" we excluded species defined by USDA as upland, facultative upland and terrestrial; thus we removed four species listed by Mills but added four new species with a net gain of zero nonindigenous to the list. We removed *Sonchus arvensis*, *Sonchus arvensis* var. *glabrescens*, *Carex flacca*, *Epilobium parviflorus*, and *Polygonum caespitosum* var. *longisetum* but added *Phalaris arundinacea*, *Phragmites australis australis*, *Salix caprea*, and *Lupinus polyphyllus*, which meet our criteria as established, nonindigenous and aquatic species.

We note several changes to the taxonomy (below) and a few changes to names in common usage. In many cases, we have revised the date of first report from that cited in Mills based on herbarium collections and other literature. Mills relied on Torrey's, 1843 "Natural History of New York" to cite the earliest report for a number of species as 'widespread by 1843'. As this work is limited to the State of New York, we revised the location of these species (*Menta spicata*, *Conium maculatum*, *Solanum dulcamara*, *Echinochloa crus-galli*, *Persicaria maculosa*, and *Poa trivialis*) from 'widespread' to New York. Similarly, Mills relied on Dudley's (1886) "The Cayuga Flora" to note three *Salix* species as

Table 7
Origin, date and location of first sighting, and vector(s) for nonindigenous aquatic plants of the Great Lakes.

Species	Common name	Origin	Date	Location	Vector
Rumex obtusifolius[b]	Bitter dock	Eurasia	1837	Adrian, Michigan	Unknown
Phalaris arundinacea[a]	Reed canary grass	circumboreal	1838	Ann Arbor, MI	Release cultivation
Agrostis gigantea[b]	Redtop	Eurasia	1838	Castle Park, MI	Release cultivation
Echinochloa crus-galli[b]	Barnyard grass	Eurasia	1838	Jackson, MI	Release cultivation
Persicaria maculosa[b]	Spotted lady's thumb	Eurasia	1838	Kalamazoo, MI	Unknown
Lythrum salicaria	Purple loosestrife	Eurasia	1839	Ithaca, NY	Canals, shipping solid ballast
Mentha spicata[b]	Spearmint	Eurasia	1843	Western NY	Release cultivation
Conium maculatum	Poison hemlock	Eurasia	1843	NY (Ontario)	Release cultivation
Mentha aquatica[b]	Watermint	Eurasia	1843	Manistee Watershed	Release cultivation
Poa trivialis	Rough-stalked Meadow grass	Eurasia	1843	New York	Release cultivation or shipping solid ballast
Solanum dulcamara	Bittersweet nightshade	Eurasia	1843	New York	Release cultivation
Nasturtium officinale[b]	Water cress	Eurasia	1847	Niagara Falls	Release cultivation
Veronica beccabunga[b]	European brooklime	Eurasia	1849	Clinton, MI	Shipping solid ballast or release cultivation
Juncus gerardii	Black-grass rush	Atlantic	1862	Chicago	Shipping solid ballast
Najas marina[b]	Spiny naiad	Caribbean	1864	Onondaga Lake	Shipping solid ballast, dispersal with migratory birds
Chenopodium glaucum	Oak leaved goose foot	Eurasia	1867	Onondaga Lake, NY	Railroad/highway
~~*Sonchus arvensis*~~	~~Field sow-thistle~~	~~Eurasia~~	~~1865~~	~~Central NY~~	~~Unintentional release~~
Carex disticha	Two-rank sedge	Eurasia	1866	Belleville, Ontario	Shipping solid ballast
Phragmites australis[a]	Common reed	Europe	1869	Presque Isle, Erie	Shipping solid ballast
Epilobium hirsutum	Great hairy willow herb	Eurasia	1874	Ithaca, NY	Unintentional release, shipping solid ballast
Typha angustifolia[b]	Narrow leaved cattail	Eurasia	1877	Detroit, MI	Unintentional release
Potamogeton crispus	Curly pondweed	Eurasia	1879	Keuka Lake	Deliberate release, release with fish
Myriophyllum spicatum[b]	Eurasian watermilfoil	Eurasia	1880	Dryden Lake	Aquarium release, ship fouling
Salix purpurea[b]	Purple willow	Eurasia	1880	South Haven, MI	Release from cultivation
Iris pseudacorus[b]	Yellow flag	Eurasia and Africa	1882	Cayuga Lake	Release from cultivation
Alopecurus geniculatus	Water foxtail	Eurasia	1882	Lake Erie	Release from cultivation
Lysimachia nummularia	Moneywort	Eurasia	1882	central NY	Release from cultivation
Rorippa sylvestris	Creeping yellow cress	Eurasia	1884	Rochester, NY	Shipping solid ballast
Salix alba[b]	White willow	Eurasia	1886	New York	Release from cultivation
Salix fragilis[b]	Crack willow	Eurasia	<1886	New York	Release from cultivation
Myosotis scorpioides	True forget-me-not	Eurasia	1886	Central NY	Release from cultivation
Lycopus asper[b]	Western water horehound	Mississippi	1892	Port Huron	Unintentional release
Puccinellia distans	Weeping alkali grass	Eurasia	1893	Montezuma, NY	Shipping solid ballast, rail/highway
Marsilea quadrifolia[b]	European water clover	Eurasia	1893	Cascadilla Creek, Ithaca, NY	Deliberate release
Myosoton aquaticum[b]	Giant chickweed	Eurasia	1894	Lake St. Clair	Unknown
Juncus compressus	Flattened rush	Eurasia	1895	Cayuga Lake	Unintentional release
~~*Carex flacca*~~	~~Sedge~~	~~Eurasia~~	~~1896~~	~~Detroit River~~	~~Unknown~~
Mentha x gracilis [*arvensis x spicata*][b]	Creeping whorled mint	Eurasia	1896	Lake St. Clair	Release from cultivation
Butomus umbellatus[b]	Flowering rush	Eurasia	1897	Montreal (Ontario)	Shipping solid ballast
Rumex longifolius	Yard dock	Eurasia	1901	Isle Royale	Release from cultivation
~~*Sonchus arvensis var. glabrescens*~~	~~Smooth field sow-thistle~~	~~Eurasia~~	~~1902~~	~~Ohio~~	~~R(A)~~
Lycopus europaeus	European water horehound	Eurasia	1903	Lake Ontario	Shipping solid ballast
Salix caprea[a]	Goat willow	Eurasia	1905	Illinois	Release from cultivation
Impatiens glandulifera	Indian balsam	Asia	1912	Port Huron	Release from cultivation
Lysimachia vulgaris[b]	Garden loosestrife	Eurasia	1912	Detroit	Release from cultivation
Pluchea odorata var. odorata[b]	Marsh fleabane	Atlantic	1912	Detroit	Unintentional release
Frangula alnus[b]	Glossy buckthorn	Eurasia	1913	Lake Ontario	Release from cultivation
Alnus glutinosa	Black alder	Eurasia	1913	widespread	Release from cultivation
Pluchea odorata var. succulenta[b]	Sweetscent	Atlantic	1914	Detroit, MI	Release from cultivation
Juncus inflexus[b]	European meadow rush	Eurasia	1922	Lake Ontario	Deliberate release
Nymphoides peltata	Yellow floating heart	Eurasia	1930	Conneaut River	Unintentional release
Najas minor	Minor naiad	Eurasia	1932	Lake Cardinal	Deliberate release
Cirsium palustre[b]	Marsh thistle	Eurasia	1934	Lawson, MI	Unknown
Cabomba caroliniana	Carolina fanwort	Southern US	1935	Kimble Lake	Aquarium release, unintentional release
Sparganium glomeratum	Bur reed	Eurasia	1936	Lake Superior	Unknown
Glyceria maxima	Reed manna grass	Eurasia	1940	Lake Ontario	Release from cultivation, shipping solid ballast
Trapa natans[b]	Water chestnut	Eurasia	1949	Seneca Lake	Unintentional release, aquarium release
Carex acutiformis	Swamp sedge	Eurasia	1951	St. Joseph Lake	Unknown
~~*Polygonum caespitosum var longisetum*~~	~~Bristly lady's thumb~~	~~Asia~~	~~1960~~	~~Ohio~~	~~Unknown~~
~~*Epilobium parviflorum*~~	~~Small-flowered hairy willow herb~~	~~Eurasia~~	~~1966~~	~~Benzie Co., MI~~	~~Unknown~~
Lupinus polyphyllus[a]	Bigleaf lupine	Western US	1959	L'Anse, MI	Intentional ornamental
Solidago sempervirens	Seaside goldenrod	Atlantic	1969	Chicago	Unintentional release
Hydrocharis morsus-ranae[b]	European frog-bit	Eurasia	1972	Lake Ontario	Aquarium release, deliberate release, ship fouling

[a] New addition.
[b] Information updated. Strike-through text indicates species that have been removed.

"widespread"; and we likewise revise the locations of these species to New York as well as adding *Salix caprea* to the list.

Of note, USDA also maintains a database of plants which includes native and non-native designations. They use Voss (1985) and other state Flora guides as their primary references. The USDA system does not allow for dual designations within floristic regions; should an area contain both native and non-native populations, these species are designated in their system as native (Pers.Com. Moore 2017). These floristic regions do not follow the pattern of glaciation, thus a number of species (*Phalaris arundinacea*, *Juncus gerardii*, *Najas marina*, *Sparganium glomeratum*, *Typha angustifolia*, *Puccinellia distans*, *Pluchea odorata* var. *succulenta*, *Cabomba caroliniana*, *Lupinus polyphyllus*, *Solidago sempervirens*) which we considered as nonindigenous within the glaciated Great Lakes region, but which are native in non-glaciated areas, appear to be native on USDA maps but are non-indigenous within the Great Lakes.

Rumex obtusifolius (bitter dock, Polygonaceae) – revised introduction

Mills identified bitter dock as widespread in the Great Lakes region by 1840. We confirm specimens for Adrian, MI in 1837 and in Ann Arbor, MI for 1838 from the University of Michigan Herbarium (2018).

Phalaris arundinacea (reed canary grass, Poaceae) added

This species has both native and introduced populations in close proximity because it is both native to North America and has had European transplants cultivated for agricultural use (Waggy, 2010). Originally considered a 'range expander' within the Great Lakes region, the European strains are now considered nonindigenous (Jakubowski et al., 2013). The European strains have been cultivated for use as livestock forage (hay) with the first confirmed collection in 1838 in Ann Arbor, MI (iDigBio, 2015). Note that USDA lists the species as native because both native and non-native populations can be found within floristic boundaries.

Agrostis gigantea (redtop, Poaceae) – revised introduction

Mills placed the earliest collection of *Agrostis gigantea* for the Great Lakes region in 1884, in Ontario in the Lake Superior watershed. We found specimen data in the University of Michigan Herbarium collection which places it in the basin significantly earlier – 1838 in Castle Park, Michigan.

Echinochloa crus-galli (barnyard grass, Poaceae) – revised introduction

Mills identified barnyard grass as widespread by 1843, with records from the Lake Ontario shoreline and assigned this species as either an introduction from solid ballast or release from cultivation. We confirmed a specimen for Jackson, MI in 1838 from the University of Michigan Herbarium (2018). Given the 1838 record is inland, we consider it more likely that this species was introduced to the Great Lakes region via a release from cultivation.

Persicaria maculosa (spotted lady's thumb, Polygonaceae) – revised taxonomy and introduction

ITIS noted the revision of the taxonomy of this species in 2011, changing the scientific name from *Polygonum persicaria* to *Persicaria maculosa*. We further note that the common name has been refined to 'spotted lady's thumb' (from simply 'lady's thumb') distinguishing the nonindigenous species from related native species also commonly called lady's thumb. Mills identified this species as widespread by 1843, with records from the Lake Ontario shoreline. We confirmed a specimen for Kalamazoo, MI in 1838 from the University of Michigan Herbarium (2018).

Mentha spp. –M. piperita, M. spicata, M. aquatica, M. gentilis, and M. x gracilis (mint, Lamiaceae) – revised taxonomy and introduction

Mills listed *Mentha piperita* (peppermint) as naturalized in western New York based on Torrey, 1843. However, *M. piperita* is a sterile hybrid of 2 non-natives, *Mentha spicata* (spearmint) and *Mentha aquatica* (watermint). We replace the sterile hybrid with the parent species *M. aquatica*, which was not listed by Mills. Although Torrey's report of *M. piperita* in western NY by 1843 suggests the parent species likely also was present, the earliest record we are able to confirm for *M. aquatica* in the Great Lakes basin is 1895 in Michigan's Black Swampland (GBIF, 2008). We are not currently tracking the sterile hybrid. *Mentha gentilis* (as it appears in Mills) is no longer recognized as a species name. This plant is now recognized as a hybrid of the native *M. arvensis* and the non-indigenous *M. spicata* and is noted as *Mentha x gracilis* in recent literature and we track it under this name. Mills reported *M. gentilis* for central New York in 1915; we are able to place this hybrid near Lake St. Clair significantly earlier in 1896 (Reznicek et al., 2011).

Nasturtium officinale (water cress, Brassicaceae) – revised taxonomy

ITIS noted the revision of the taxonomy of this species in 2011, changing the scientific name from *Rorippa nasturtium-aquaticum* to *Nasturtium officinale*.

Veronica beccabunga (European brooklime, Scrophulariaceae) – revised introduction, added vector

The first report of *V. beccabunga* is revised to be significantly earlier with discovery of a specimen in the University of Michigan collections dated to 1849 in Clinton, Michigan in the Lake Huron drainage. Because this specimen was found in wetlands near a cemetery, we consider escape from an ornamental planting to be the most likely source for this first introduction to the Great Lakes region, though other populations may have started from solid ballast. In contrast, Mills dated the species to 1915 in New York.

Juncus gerardii (black-grass rush, Juncaceae) – note on status

We continue to list black-grass rush as nonindigenous following Mills. Note, however, USDA currently treats this species as native throughout North America. Their determination is "based on the Flora of North America series which treats this species as native throughout North America". However, USDA acknowledges that Voss (1985) indicated that the species is "quite probably not indigenous in Michigan" and is investigating the designation (Pers. Com., Moore 2017).

Najas marina (spiny naiad, Najadaceae) – revised origin

N. marina is now considered to be a cosmopolitan species that may have invaded from the Caribbean via solid ballast or with migratory birds rather than from Eurasia (Agami and Waisel, 1986). We note that USDA currently treats this species as native throughout North America. Their determination is based on the Flora of North America series which treats this species as native throughout North America. However, USDA acknowledges that Voss' (1985) statement that it was first collected in 1938 suggests it is non-native in Michigan (Pers. Com., Moore 2017). We concur with Mills earlier placement of the species in Onondaga Lake by 1864.

Carex disticha (two-rank sedge, Cyperaceae) – note on common name

We note the common name 'two-rank sedge' has come into common usage for this species.

Phragmites australis australis (common reed, Poaceae) - added

With recent taxonomic revision officially separating this organism into subspecies, we list *Phragmites australis australis* as non-indigenous to the Great Lakes, and note that the native is now

officially *Phragmites australis americanus*. Despite the name, *Phragmites australis australis* is believed to have originated in the Middle East and to have invaded the US via solid ballast (Swearingen and Saltonstall, 2010). Our earliest confirmed report of the non-native subspecies in the Great Lakes basin dates to 1869 in Erie, PA (GBIF, 2008).

Typha angustifolia (narrow-leaved cattail, Typhaceae) – revised introduction

We continue to list this species as nonindigenous based on evidence presented by Mills that it was likely introduced by the earliest settlers on the east coast. We are able to confirm that not only was *T. angustifolia* present in central New York by the 1880s, but we have one report of the species in the Lake Michigan drainage for 1877 (University of Michigan Herbarium). Note USDA maps the species as native throughout North America citing Flora of North America and Voss (1985) as being equivocal regarding species' nativity, but acknowledging a need to re-evaluate the species nativity status as a whole (Pers. Com. Moore 2017).

Myriophyllum spicatum (Eurasian watermilfoil, Haloragaceae) – revised introduction

We significantly revise the earliest record for Eurasian watermilfoil (from 1952) with a collection of the species in Dryden Lake (Lake Ontario drainage) in 1880 (Mississippi Herbarium Consortium, 2013).

Salix spp. – S. alba, S. fragilis, S. purpurea, and S. caprea (willow, Salicaceae) – added 1 species, revised introductions*

Mills placed 3 nonindigenous willow species, *S. alba*, *S. fragilis* and *S. purpurea*, as widespread in the Great Lakes basin by 1886. We confirm an earlier record for *S. purpurea* in South Haven, Michigan in 1880 (University of Michigan Herbarium) and confirm Mills' dates for *S. alba* and *S. fragilis*. We add *Salix caprea* as meeting our criteria and confirm a similarly early record of this small willow in 1905 in Chicago, Illinois (Field Museum collection). Like the other willows, this species is commonly cultivated, currently sold in the Great Lakes region, and assumed to have escaped cultivation.

Iris pseudacorus (yellow flag, Iridaceae) – revised introduction

We revise the first report for *I. pseudacorus* a few years earlier with a report for Cayuga Lake in 1882 (GBIF, 2008) in contrast to the Mills date of 1886 in Ithaca. We also note that this species is now considered native to Africa in addition to Eurasia.

Lycopus asper (western waterhorehound, Lamiaceae) – revised introduction

Mills places the first report of L. *asper* in Lake Erie in 1892, but we note a concurrent confirmed report of the species just upstream in Port Huron, MI (Lake St. Clair drainage) (Stuckey, 1969) and revise the location to the upstream site as the more likely point of introduction.

Puccinellia distans (weeping alkali grass, Poaceae) – taxonomic note

We continue to list this species as nonindigenous to the Great Lakes following Mills. The USDA separates Great Lakes populations of the species as *Puccinellia distans* ssp. *distans* (nonindigenous throughout the Great Lakes) and *Puccinellia distans* ssp. *borealis* (nonindigenous, present in Wisconsin and New York), but also notes possibly native populations of the parent species in the region.

Marsilea quadrifolia (European waterclover, Marsileaceae) – revised introduction

We revise the first report for *M. quadrifolia* significantly earlier to 1893 in Cascadilla Creek near Ithaca, NY (Lake Ontario drainage) (Johnson, 1986) in contrast to the Mills report from 1925 in Cayuga Lake. USDA currently lists this species as native in the province of Ontario, but plans to revise that status to introduced (Pers. Com., Moore 2017).

Myosoton aquaticum (giant chickweed, Caryophylliaceae) – revised taxonomy

ITIS noted the revision of the taxonomy of this species in 2011, changing the scientific name from *Stellaria aquatica* to *Myosoton aquaticum*.

Butomus umbellatus (flowering rush, Butomaceae) – revised introduction

Mills places this species in the Detroit River by 1930. We revise the first report for *B. umbellatus* significantly earlier confirming a report noted by Mills of the species across from Montreal in 1897. We have also confirmed additional reports for this species in the Detroit River as early as 1905.

Lysimachia vulgaris (garden loosestrife, Primulaceae) – revised introduction

We use a specimen of this species from the Michigan State Herbarium collection from 1912 in Detroit to place the introduction just a year earlier. However, this suggests the distribution was already widespread given the record for the species noted by Mills the following year in Lake Ontario.

Pluchea odorata - var. odorata and var. succulenta (marsh fleabane and sweetscent, Asteraceae) – revised introductions and vectors

Pluchea odorata var. *purpurescens* has been revised to *P. odorata* var. *odorata* (considered just a color morph of the type species rather than a separate subspecies). In the Great Lakes region, the common name has been shortened to marsh fleabane (rather than salt-marsh fleabane). Mills placed the earliest record for this subspecies at 1916 in Lake Erie. A specimen from the University of Michigan Herbarium collection places this upstream in the Detroit vicinity in 1912. The vector for this species is revised from unknown to unintentional release, given the location's association with salt waste.

P. odorata var. *succulenta* is now commonly known as 'sweetscent'. The first report for *P. odorata v. succulenta* has been revised significantly earlier to 1914 with a report from Detroit, Michigan (Lake St. Clair drainage) in the University of Michigan Herbarium records. This brings the date of first introduction for this subspecies to the same timeframe as the type species. The USDA maps this subspecies as native to the US, but invasive in the province of Ontario. Because USDA currently maps ranges that are comprised of native and non-native populations as native, it is likely the northern populations within the Great Lakes states that are within the glaciated areas are nonindigenous to the region. (Pers. Com., Moore 2017). We continue to separately track the two nonindigenous subspecies of *P. odorata* in the Great Lakes.

Juncus inflexus (European meadowrush, Juncaceae) – revised vector

The common name of this species is European meadow rush. Its introduction is now attributed to deliberate release (USEPA, 2008b) rather than unknown.

Frangula alnus (glossy buckthorn, Rhamnaceae) – revised taxonomy

Historically, buckthorn taxonomy has been controversial. However, more recent genetic research supports the separation of *Frangula* species, including glossy buckthorn, from the *Rhamnus* genus (Bolmgren and Oxelman, 2004). This shift does not yet appear in ITIS, but has been accepted by USDA.

Cirsium palustre (marsh thistle, Asteraceae) – revised introduction

Mills placed the earliest records of *Cirsium palustre* in the Lake Superior watershed prior to 1950. We are able to confirm a report for 1934 for the Lake Superior watershed in Lawson, Michigan based on University of Michigan Herbarium specimens.

Cabomba caroliniana (Carolina fanwort, Cabombaceae) – note on status

The common name of this species is now noted as Carolina fanwort. USDA currently maps this species as native, but acknowledges that the Flora of North America and Voss (1985) treat it as non-native in Michigan and likely occurrences in the Great Lakes region should be treated as non-native (Pers. Com., Moore 2017).

Sparganium glomeratum (bur reed, Sparganiaceae) – note on status

We concur with Mills that the patchy distribution of *Sparganium glomeratum* is indicative of a non-native species. Although, USDA lists the species as native in MN and WI (absent in the rest of the Great Lakes states and Ontario) based on the Flora of North America series which treats this species as native throughout North America, populations within the Great Lakes basin glaciated region are disjunct from the native range (Pers. Com., Moore 2017).

Glyceria maxima (reed manna grass, Poaceae) – note on common name

The common name of this species has changed from reed sweet-grass to reed manna grass.

Trapa natans (water chestnut, Trapaceae) – revised introduction

The first report for this species is revised earlier to 1949, in Seneca Lake in the Lake Ontario drainage (North Carolina State University Herbarium; Madsen, 1990). Mills had reported it as in Lake Ontario tributaries by 1959.

Lupinus polyphyllus (bigleaf lupine, Fabaceae) - added

The ornamental plant bigleaf lupine is considered established in large portions of the Lake Superior basin. The earliest confirmed report for this species outside cultivation in the Great Lakes basin is in L'Anse, Michigan in 1959 (University of Michigan Herbarium). Currently, USDA maps this species as native, but acknowledges that Voss (1985) treats it as introduced in Michigan and recommends that occurrences in the Great Lakes region be treated as non-native (Pers. Com,. Moore 2017).

Solidago sempervirens (seaside goldenrod, Asteraceae) – note on status

We continue to list this species as nonindigenous. The USDA maps the species as native, but acknowledges that both Flora of North America and Voss (1985) treat it as introduced and recommend that occurrences in the Great Lakes region be treated as nonindigenous (Pers. Com. Moore 2017).

Hydrocharis morsus-ranae (European frogbit, Hydrocharitaceae) – vectors assigned

Mills had not assigned this species to a particular entry mechanism. We consider it to most likely have been an aquarium release, whether accidentally (U.S. EPA, 2008b) or deliberately, but cannot rule out the possibility that it was introduced via fouling of ships or recreational boats.

Characterization of vectors, temporal patterns and origins

Mills' seminal work lists 137 established aquatic species as nonindigenous to the Great Lakes (two plants are further subdivided into two subspecies groups). We have removed 7 of these species: 3 have been redefined as probably native and 4 plants (including both subspecies of *Sonchus arvensis*) have been reclassified as terrestrial. Thirty-five species that arrived prior to 1993 (some due to reclassification, some due to a time lag in discovery and reporting) have been added to the list. Twenty-four new species have invaded post-1993, bringing the total to 188 (with *Pluchea odorata* including two subspecies). Notably, 21 of the 23 species were introduced between 1993 and 2006, but only 3 new species have been introduced in the last decade.

Mills reported a taxonomically diverse assemblage somewhat dominated by aquatic plants (42%). The assemblage remains diverse; through the addition of several non-plant species and removal of 4 terrestrial plant species, plants have fallen to 31% of the total number of nonindigenous species overall, but remain the largest taxonomic group (Fig. 1). Great Lakes nonindigenous taxa have seen substantial gains in Crustacea (formerly 4%, now 13%), microbes (formerly 2%, now 8%) and other invertebrate categories (formerly 6%, now 10%) in the 25 years since Mills published their original analysis. The 24 species introduced post-1993 are dominated by small-bodied organisms, including 8 copepods, 3 testate amoebae, 3 viruses, 2 cladocerans, 1 alga, 1 bacteria, 3 protozoan parasites, a cestode, a tapeworm and an amphipod.

Mills reported a nonindigenous assemblage dominated by species native to Eurasia (53%) and the Atlantic coast of the US (11%); this remains the case for the modern assemblage, shown in Fig. 2.

Using the vector categories set forth by Mills (called 'entry mechanisms' in the original work), we assigned all species to a 'most probable' vector. As noted individually above, shifts in the location of first record reassigns the 'most probable vector' for several species and many species that Mills categorized as 'unknown' have been assigned vectors based on newer information. While Mills' concluded that shipping, with 41 species, was the leading vector, we find that 54 of his taxa (a handful of early solid ballast introductions, but mostly those originally attributed as unknown) should have been attributed as Unintentional Release (most in the sub-category of 'escaped cultivation'). Nonetheless, with the addition of pre-1993 invaders not included in Mills, along with post-1993 invaders, we find that shipping remains the leading vector of introduction (68 species, representing 36% of introductions) (Fig. 3).

Introductions follow distinct temporal patterns and particular taxonomic groups are associated with each 'wave' of invasion, as shown in Figs. 4–6. Prior to 1844, eleven emergent/facultative plants are documented to have become established having escaped cultivation (or as weed species likely transported as a seed contaminant), with the earliest documented nonindigenous species of the region listed as *Rumex obtusifolius* (bitterdock) in 1837.

The following 25 years see the rapid rise of vectors associated with transportation, including canals, railways, and solid ballast. This period sees the introduction of the first non-indigenous mollusk (*Elimia virginica* via the Erie Canal in 1860), the first fish (*Petromyzon marinus* invading Lake Ontario in 1863), and the first submerged plant (*Najas marina* inland in the Ontario drainage in 1864). The rate of introduction during this segment (25 year period) is just 0.36 species per year.

Deliberate planting started with *Oncorynchus tshawytscha* (chinook salmon) in Lake Huron in 1870. In 1902, the first microbe (furunculosis) was found as a hitchhiker with stocked fish, and 1929 marks the introduction of a parasitic fluke (*Ichthyocotylurus pileatus*). Between 1869 and 1943, 78 species are introduced deliberately or accidentally via stocking, escape from cultivation, canals and solid ballast (or hitchhiking with other organisms in those vectors). The rate of introduction during this period 75-year period averages 1.04 species/year.

The first report of *Stephanodiscus binderanus* (perhaps not coincidentally the first nonindigenous alga) in Lake Erie in 1930 is the vanguard in the next wave attributed to introduction via ballast

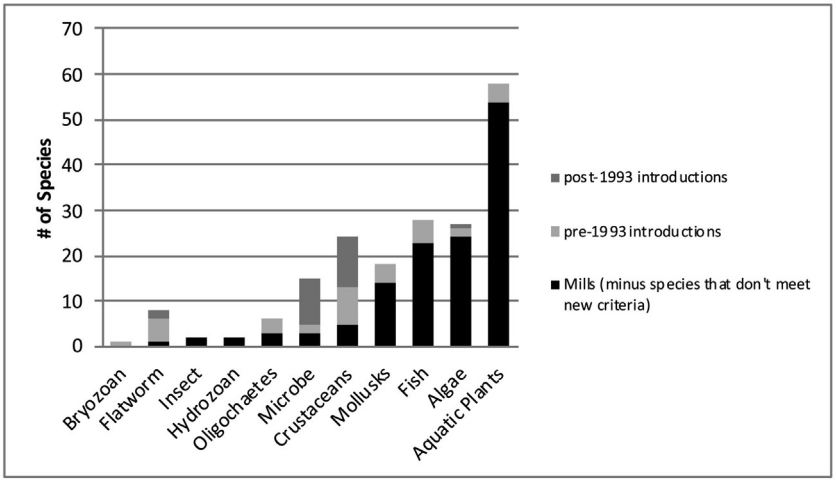

Fig. 1. Taxonomic diversity of nonindigenous species established in the Great Lakes between 1838 and 2018.

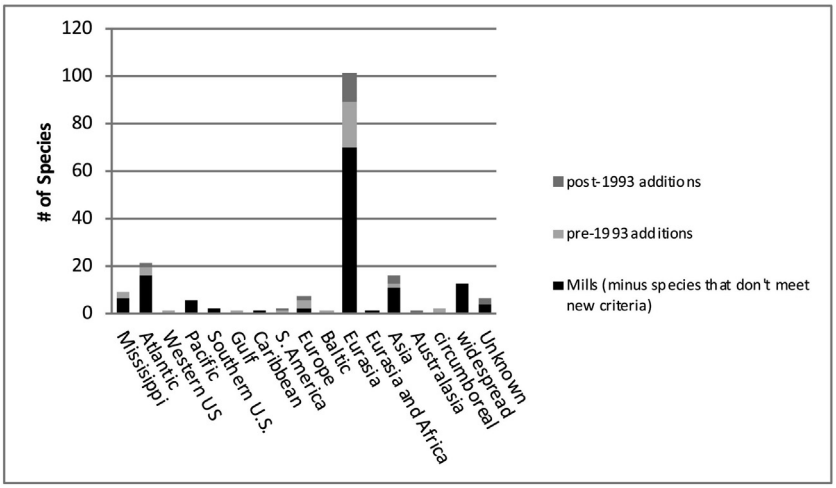

Fig. 2. Origin of nonindigenous species established in the Great Lakes between 1838 and 2018.

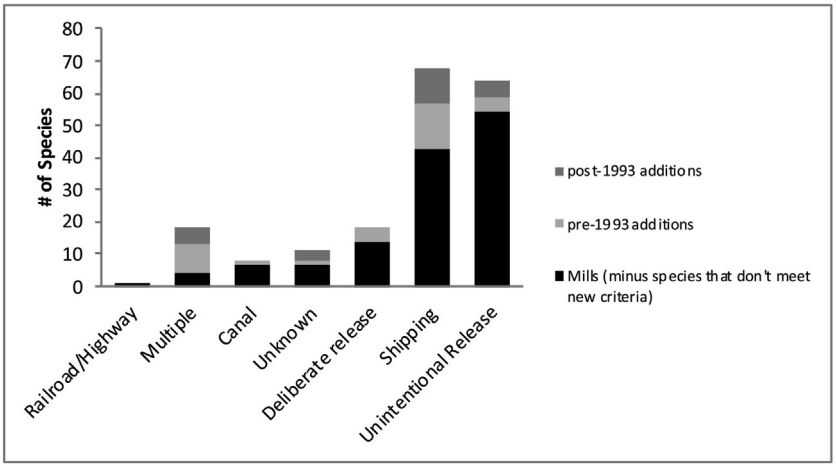

Fig. 3. Vectors for nonindigenous species.

water. Introduction via other vectors gradually declines and ballast water rapidly takes the lead accounting for 40 of the 72 species (55%) introduced between 1944 and 1993. Algae, invertebrates, crustaceans and microbes dramatically increase in frequency among the nonindigenous assemblage during this period, though mollusks, plants and fish are also attributed to ballast water

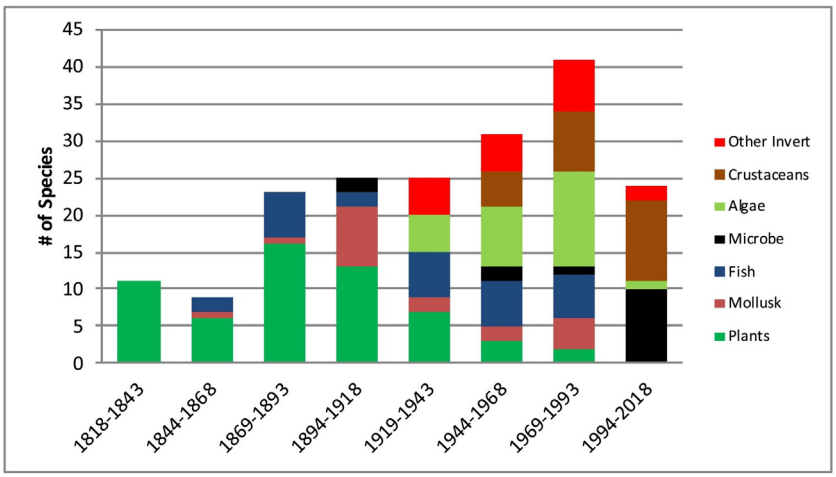

Fig. 4. History of nonindigenous species introductions by taxa.

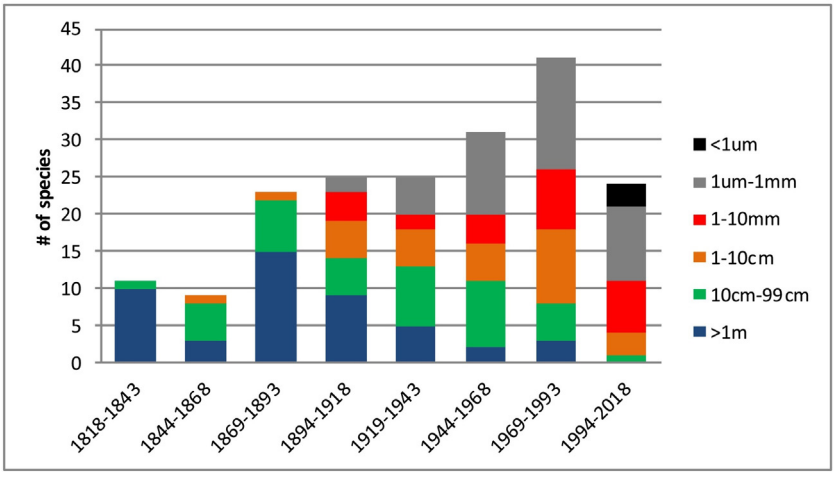

Fig. 5. History of nonindigenous species introductions by organism size.

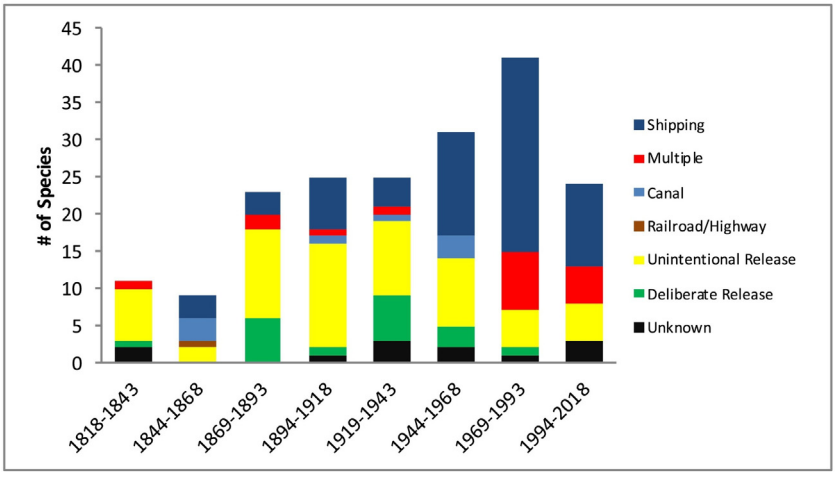

Fig. 6. History of nonindigenous species introductions by vector.

releases. The rate of introduction during this 50-year period averages 1.4 species per year.

Mills noted an almost linear trend in the number of new introductions within each 30 year period of their analysis. Our re-analysis of the pre-1993 period in 25 year increments shows the same linear trends within each corresponding segment (as expected). The minor shifts to dates for particular species did not make a significant difference in this historic pattern. In sharp

contrast, we find the number of introductions post-1993 to have returned to approximately the same rate as pre-1968. Only 24 new species have been introduced since 1993 in contrast to 42 in the previous 25 years. This is unlikely to be accidental. Under the authority of the Nonindigenous Prevention and Control Act of 1990, the U.S. Coast Guard began requiring ballast water exchange for vessels entering the Great Lakes in 1993. It should be noted that the largest reduction of introductions has been among organisms attributed to shipping (58% reduction).

Early introductions were primarily cultivated plants and fish, including both those stocked deliberately and those which unintentionally escaped cultivation (Fig. 6). More recent invaders are primarily small. In the last 25 years, the most progress has been made with reducing the number of introductions of organisms >1 cm in size (77% reduction). In contrast, the number of introductions of organisms <1 cm in size has been reduced by only 13% (Fig. 5).

To take a finer-scale look at the changes that occurred between these last two 25-year periods, and to better understand whether this change was sudden or gradual and whether improvements continue to be made in recent history (within the last 25 years), we look to the cumulative number of invasive species by vector since 1969 (Fig. 7). In the 25 years prior to implementation of ballast regulations in 1993, the introduction rate was 1.68 species per year with 62% of the species introduced attributed to ballast water. 1993 marks the start of the requirement for ballast water exchange, and 2006 marks the start of the requirement to flush tanks containing residual sediment with seawater. The intervening period (exchange only) still had an introduction rate of 1.61 species per year, with only a slightly lower portion attributed to ballast (52%). The period during which both exchange and flushing of sediments was required (2006–2018) had an introduction rate of only 0.27 species per year with none of these introductions attributed to ballast. Only three species meeting our criteria were documented as established during this period: *Thermocyclops crassus* in Shea et al., 2014, *Diaphanosoma fluviatile* in 2015 and *Mesocyclops pehpeiensis* in 2016. While currently attributed as unknown vector, both of these are thermophilic copepods established elsewhere in the U.S. and were unlikely to have been introduced to the Great Lakes via ballast.

Discussion

Mills noted that little was known about how their 139 exotic species 'fit' into modern Great Lakes communities and speculated that about 10% of these species had demonstrably substantial impacts on the Great Lakes, with the fishes having more important ecological and economic effects. That work cautioned that concluding the other 90% to be inconsequential would be erroneous noting 'the effects may simply not have been studied'. We find significantly more evidence for impacts of these species (Sturtevant et al., 2014) than Mills, with at least 31% of species having measurable socioeconomic or environmental impacts. Note that this methodology separately considers beneficial impacts, but makes no attempt to calculate a 'net' influence, merely noting that about one-third of the nonindigenous species with measureable negative environmental or socioeconomic impacts also have measureable benefits. The current list of significantly impactful species includes broader representation across taxa; damaging invaders include fish, plants, mollusks, crustaceans, algae and microbes. To Mills' list of 13 species with 'demonstrably substantial impacts on the Great Lakes' (sea lamprey, alewife, purple loosestrife, chinook salmon, brown trout, common carp, coho salmon, furunculosis, *Glugea hertwigi*, white perch, Eurasian watermilfoil, zebra mussel, and Eurasian ruffe) we add 40 species that also invaded prior to 1993 and now have measurable impacts and are therefore considered to be "invasive": *Echinochloa crus-galli*, *Persicaria maculosa*, *Conium maculatum*, *Solanum dulcamara*, *Juncus gerardii*, *Bithynia tentaculata*, *Epilobium hirsutum*, *Oncorhynchus mykiss*, *Typha angustifolia*, *Potamogeton crispus*, *Iris pseudacorus*, *Salix x fragilis*, *Juncus compressus*, *Butomus umbellatus*, *Osmerus mordax*, *Lysimachia vulgaris*, *Rhamnus frangula*, *Juncus inflexus*, *Ulva intestinalis*, *Lepomis microlophus*, *Ichthyocotylurus pileatus*, *Nymphoides peltata*, *Stephanodiscus binderanus*, *Scardinius erythrophthalmus*, *Najas minor*, *Cirsium palustre*, *Cabomba caroliniana*, *Actinocyclus normanii f. subsalsa*, *Trapa natans*, *Carex acutiformis*, *Renibacterium salmoninarum*, *Myxobolus cerebralis*, *Cylindrospermopsis raciborskii*, *Hydrocharis morsus-ranae*, *Nitellopsis obtusa*, *Glyceria maxima*, *Corbicula fluminea*, *Bythotrephes longimanus*, *Dreissena rostriformis bugensis*, and *Potamopyrgus antipodarum*. Recent invaders (post-1993) with significant impacts add 8 to the list including *Echinogammarus ischnus*, *Cercopagis pengoi*, viral hemorrhagic septicemia virus, *Heterosporis sutherlandae*, *Ranavirus sp.* (Largemouth Bass Virus), *Rhabdovirus carpio* (spring viremia of carp), *Piscirickettsia* cf *salmonis* (muskie pox), and *Ulva flexuosa*, for a total of 61 species with measureable impact.

Using this more extensive list of invasive species (Fig. 8), we still clearly note the first wave of these impactful species highlighted by Mills that occurred in the mid-to-late 1800s and was associated with deliberate introductions, solid ballast and canals. The invasion rate during this period (1868–1887) was 1.05 species

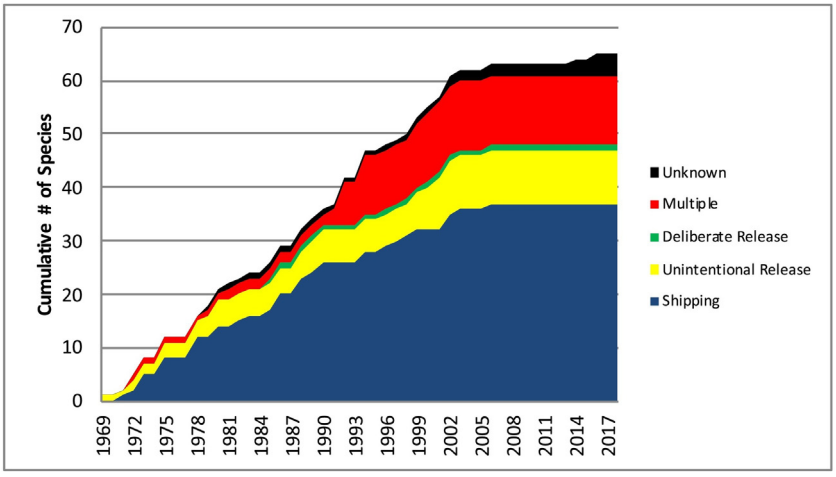

Fig. 7. Recent history of nonindigenous species introductions by vector.

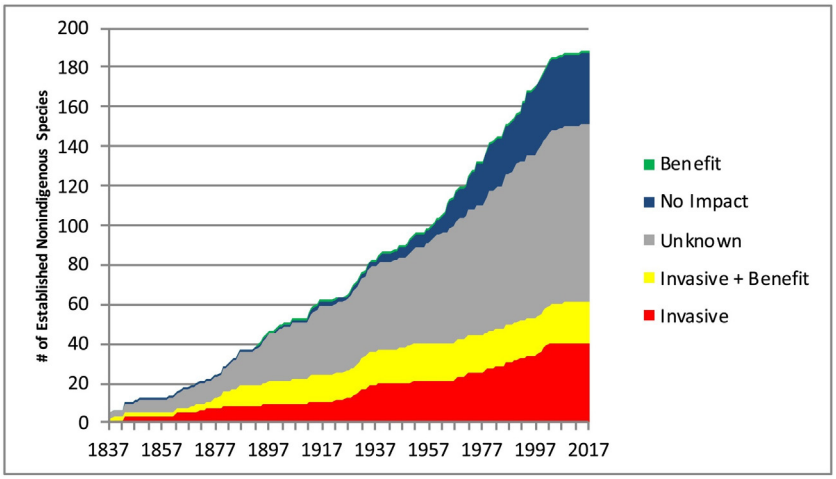

Fig. 8. A history of nonindigenous species introductions by impact.

per year, and this wave comprised 11% of total established species (20/188) but 20% of invasive species (12/61). Mills suggested a second wave starting in 1933 that was associated with ballast water, fish stocking, and unintentional releases. In our analysis, this resolves into two separate waves – a brief but significant wave from approximately 1925–1940 dominated by deliberate fish stocking and unintentional releases from cultivation, and a third longer wave from 1959 to 2002 dominated by ballast introductions (Grigorovich et al., 2003a, 2003b; Holeck et al., 2004). This third wave appears to have ended in 2006 with the implementation of regulations requiring flushing of tanks carrying residual ballast sediments. The second wave's invasion rate was 1.53 species per year and included 12% of established species but 20% of invasive species. The third (most recent) wave had an invasion rate of 1.81 species per year and comprised 44% of established species (82/188) but 31% (19/61) of invasive species. The third wave thus appears to account for the greatest percentage of species with significant measureable impacts (31% of the total invasive species in the Great Lakes arrived during the third wave) despite time lags between introduction and realized impact. In contrast, the inter-wave periods (pre-1867, 1888–1924, 1941–1958 and 2002–2018 – totaling 99 years) have an overall average invasion rate of just 0.65 species per year and combined account for just 34% of total established species and 29% of invasives. A return to the relatively low invasion rate of an inter-wave period (<0.65 species per year) since 2006 confirms the ending of the most recent wave.

Based on the inflection of the invasion rate curve coinciding with 2006, we attribute the ending of the third invasion wave to the implementation of ballast exchange requirements addressing vessels declaring 'no-ballast-on-board.' Previous studies conducted only a decade ago (Drake and Lodge, 2007) failed to detect a decline in invasion rate attributable to ballast regulation. We do not yet have sufficient data to examine the alternative hypothesis that significant time lags in discovery reflect a delayed response to earlier ballast water regulations. It remains possible that a phase of 'invasional meltdown' in which ballast-mediated invasions in the first part of the third wave and subsequent alterations of the ecosystem may have facilitated the higher invasion rates of the second part of the third wave (Ricciardi, 2001; Holeck et al., 2004), offsetting any distinct decrease in invasion rate with the earlier ballast water exchange requirements under NANPCA/NISA. Likewise, we have not examined more recent vessel traffic records to fully investigate the alternative hypothesis that alterations to vessel traffic patterns resulted in reduction in propagule pressure; however, Grigorovich et al. (2003a, 2003b) note that formal records of ballast water discharge are a poor predictor of the extent of ballast-mediated invasions in the Great Lakes. Thus, we are cautiously optimistic that the recent reduction of invasion rate reflects a success of the current regulatory framework, but can only note that the rate of invasion has fallen to the equivalent of an inter-wave period, not that it has fallen to zero. While there have been no new introductions attributed to ship ballast in the last decade, that could change with any alteration of the regulatory framework or with a rise of activity in other vectors.

Conclusions

1) One hundred eighty-seven nonindigenous aquatic species have been identified as established in the Great Lakes. These species are taxonomically diverse and most have come from Eurasia (55%).
2) The Great Lakes have been subject to introductions of aquatic species since at least the early 1800s. Three primary waves are responsible for most of the invasive species with rates of introduction significantly higher than intervening stable periods.
3) The third and most recent wave of introductions (~1959–2001) had the highest rate of introductions (1.81 species per year) and was attributed to ballast water.
4) Over the most recent 25 years, the rate of introduction of nonindigenous species capable of becoming established has fallen. With the 2006 expansion of ballast regulations to include residual ballast sediments in vessels declaring 'No Ballast on Board', the rate of new invasions has fallen to a low of only 0.27 species per year.
5) Over 30% of nonindigenous species have now been demonstrated to have measurable environmental or socioeconomic impacts and are therefore considered to be invasive.

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