Impacts of Aquatic Nonindigenous Invasive Species on the Lake Erie Ecosystem

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Lake Erie is particularly vulnerable to the introduction and establishment of aquatic nonindigenous invasive species (NIS) populations. A minimum of 144 aquatic NIS have been recorded in the Lake Erie basin including several species [e.g., Eurasian watermilfoil (Myriophyllum spicatum); zebra mussel (Dreissena polymorpha); quagga mussel (Dreissena bugensis); an amphipod (Echinogammarus ischnus); round goby (Neogobius melanostomus); and sea lamprey (Petromyzon marinus)] that have had discernible impacts on the lake's ecology.

NIS pose threats to the Lake Erie ecosystem for a variety of reasons including their ability to proliferate quickly, compete with native species, and transfer contaminants (e.g., PCBs) and disease through the food web. Six of the 14 beneficial use impairments listed in Annex 2 of the Great Lakes Water Quality Agreement are impaired in Lake Erie, in part as a result of the introduction of NIS. The Lake Erie Lakewide Management Plan (LaMP) has adopted an ecosystem approach to restore beneficial use impairments in the lake. Furthermore, a research consortium, known as the Lake Erie Millennium Network, is working alongside the LaMP, to address research problems regarding NIS, the loss of habitat, and the role of contaminants in the Lake Erie ecosystem.

Key Words: nonindigenous invasive species, Lake Erie ecosystem, Lake Erie Lakewide Management Plan, phytoplankton, zooplankton, benthic invertebrates, fish, molluscs, management, round goby.

Background

At least 150 nonindigenous invasive species (NIS), representing various trophic levels, have become established in the Laurentian Great Lakes Basin since the early 1800s (Mills et al. 1993; Hall and Mills 2000; Leach 2001; Ricciardi 2001). There have been 144 aquatic NIS recorded in the Lake Erie basin including 3 disease pathogens, 2 fungi, 20 algae, 8 submerged plants, 39 marsh plants, 5 trees and shrubs, 33 invertebrates and 34 fishes (Corkum and Austen 2001). Of the NIS species in Lake Erie, 42% have become established since 1950 (Leach 2001).

Lake Erie is particularly vulnerable to NIS invasions due to its geographical location; differentiated basin morphometry, thermal regimes, chemistry and productivity which provide a multitude of habitats for native and NIS; large human population; and the high volume of shipping traffic and consequent ballast water discharges at, or upstream of, Lake Erie ports (MacIsaac 1999). Lake Erie has three basins, which vary in depth (from an average of 7.4 m in the western basin to 25 m in the eastern basin), with the western basin being more turbid, nutrient-rich, and productive

than the central or eastern basins (Lake Erie LaMP 2000). A minimum of 29 nonindigenous invasive species, in the Great Lakes Basin, were first documented in the Lake Erie Basin (including Lake St. Clair) (MacIsaac 1999). Several of these species [e.g., zebra mussel (D. polymorpha); quagga mussel (D. bugensis); an amphipod (E. ischnus); Eurasian watermilfoil (M. spicatum), round goby (Neogobius melanostomus), and sea lamprey (Petromyzon marinus) have had discernible impacts on the lake's ecology.

Lake Erie Lakewide Management Plan

In the revised Great Lakes Water Quality Agreement (GLWQA) of 1978, as amended by the Protocol signed in 1987, Canada and the United States agreed to develop and implement Lakewide Management Plans (LaMPs) for lake waters (International Joint Commission 1994). The LaMPs were established to identify critical pollutants that impair beneficial uses and develop recommendations, strategies and policy options to restore these beneficial uses (Lake Erie LaMP 2000). The hope is that the LaMPs will provide one route to "restore and maintain the chemical, physical, and biological integrity of the waters of the Great Lakes Basin Ecosystem", which is the purpose of the GLWQA.

Fourteen beneficial use impairments are listed in Annex 2 of the Great Lakes Water Quality Agreement (International Joint Commission 1994). Eleven beneficial uses are impaired in Lake Erie; of these, six beneficial uses are impaired, in part, due to nonindigenous species invasions:

- degradation of aesthetics (e.g., excessive zebra mussels on shoreline areas, Microcystis blooms);
- degradation of phytoplankton/zooplankton populations (attributed to zebra and quagga mussel grazing andhigh planktivory);
- degradation of fish populations (due to loss of native species and forage fish availability);
- loss of fish habitat [attributed to carp (Cyprinus carpio); purple loosestrife (Lythrum salicaria); common reed (Phragmites australis)];
- degraded benthos;
- and degraded wildlife populations and loss of wildlife habitat

Nonindigenous invasive species may also be contributing to other beneficial use impairments (i.e., restrictions on fish and wildlife consumption, bird or animal deformities or reproductive problems) through accumulation and biomagnification of contaminant loads, although more research is needed in this area (Jentes 1999; Charlebois et al. 2001).

Aquatic NIS Species and the Lake Erie Ecosystem

Nonindigenous invasive species and their effects on the food web have been identified as a critical issue for the Lake Erie LaMP. The introduction of the zebra mussel into Lake St. Clair and Lake Erie in the late 1980s, its subsequent dispersal throughout the Great Lakes system, and its effects on aquatic ecosystems (e.g., reduced pelagic productivity, changes in contaminant dynamics, reductions in phytoplankton and the extirpation of many native unionids through biofouling habits) illustrate the dramatic ecosystem changes that can occur with the introduction of one highly invasive species (Dahl et al. 1995; Morrison et al. 1995; Schloesser et al. 1996; Dermott and Kerec 1997; Steward et al. 1998; Makarewicz et al. 1999). The cascade effects of NIS on various trophic levels in this lake, and others in the Great Lakes Basin, underscore the need for further research and management action to curtail or reduce additional NIS introductions into both aquatic and terrestrial systems in the Great Lakes Basin. Some priority aquatic invasive species that have been identified by the Lake Erie LaMP include dreissenids (zebra and quagga mussels), round goby, spiny water flea (Bythotrephes longimanus, formerly B. cederstroemi), common reed, sea lamprey, and Eurasian watermilfoil.

Contribution of Aquatic NIS to Beneficial Use Impairments in Lake Erie

This update will focus on aquatic NIS species in Lake Erie that are of known management concern and are affecting the following beneficial use impairments: degradation of aesthetics and degradation of phytoplankton, zoo-

plankton, benthic invertebrates, and fish populations. Contributions of NIS to the loss of fish and wildlife habitat are outlined briefly elsewhere (LaMP 2000; LaMP 2002).

Degradation of Aesthetics

Nonindigenous invasive species are contributing to various aesthetic problems on Lake Erie, including massive numbers of zebra mussel shells on public beaches, fish die-offs [alewife (Alosa pseudoharengus), round goby, white perch], and algal blooms. Recent *Microcystis aeruginosa* (a large, toxic, colonial blue-green algae) blooms in the

western basin have occurred in areas where zebra mussels are well established (Lake Erie LaMP 2000; Budd et al. 2001). Vanderploeg et al. (2001) suggest that zebra mussels have induced a shift in algal abundance by ingesting all algae except *Microcystis*, which is ejected back into the water column with mussel pseudofeces. Dense *Microcystis* blooms, along with hot, calm weather probably were responsible for anoxia in the western basin of Lake Erie in late summer 2001 (R. Knight, pers. comm.). Microbial breakdown of fecal production by zebra mussels has also been implicated as contributing to a re-occurrence of anoxic phenomena in the deepest parts of central Lake Erie (R.E.J. Smith, pers. comm.).

Phosphorus concentrations have also rebounded in the west, west central, and central basins of Lake Erie by almost 10 ugP/L. Some of the concentrations in the central basin during 2000 approximated those in the early years of phosphorus controls. Phosphorus increases may be a result of decreased growth rate of mussel populations (resulting in nutrient recycling back into the water column). The roles of dreissenids and other exotic species in the recent phosphorus variations are poorly understood (M. Charlton, pers. comm.; LaMP 2002), however, external phosphorus loadings alone do not explain the increasing phosphorus concentrations reported in Lake Erie (D. Dolan, pers. comm.).

Degradation of Phytoplankton and Zooplankton Populations

Phosphorus reduction programs on Lake Erie, particularly in the western basin, have resulted in a shift in phytoplankton community species composition from those typical of eutrophic environments to those typical of mesotrophic environments. Since the invasion of dreissenid mussels, phytoplankton abundance has declined in all three basins (Munawar et al. 1999); effects are most noticeable in the eastern basin and some nearshore areas where phytoplankton biomass is now lower than would be predicted from phosphorus loads.

The switch from solid ballas to liquid ballast used on ships entering the Great Lakes system in the late 1800s has resulted in a corresponding increase in the relative and absolute importance of invertebrate, phytoplankton, and non-indigenous fish species compared to plants and insects in the Great Lakes Basin (MacIsaac 1999). Several invertebrate NIS are now present in Lake Erie including *Dreissena veligers* and *Bythotrephes. longimanus*, a large predatory zoo-plankton that preys on smaller zooplankton. Changes in the zooplankton community, like the phytoplankton community, have been most dramatic in the eastern basin of Lake Erie. Changes in zooplankton communities include the loss of dominant cold-water species in the eastern basin (e.g., *Mysis relicta*) coincident with the expansion of another nonindigenous, planktivorous fish, rainbow smelt (*Osmerus mordax*); a reduction in zooplankton mean size to less than 0.8 mm (which is indicative of heavy predation, an out-of-balance fish community, and impaired trophic transfer) in the eastern and central basins; and the NIS *B. longimanus* acting as an energy sink in the west central basin. The latter problem occurs because the prey fish community, with the possible exception of alewife and round gobies, is poorly adapted to eating *Bythotrephes* and, therefore, much of the energy is not transferred up the food chain.

Due to declines in the number and abundance of some key species in the phytoplankton and zooplankton community, the pelagic food web of Lake Erie has fewer energy resources to support organisms in higher trophic levels.

Recent Invasions

During the last 15 years, Lake Erie likeother Great Lakes, has experienced a wave of invertebrate invasions — including the arrival of zebra mussels and quagga mussels and several zooplankton species (e.g., *B. longimanus*, *Cercopagis pengoi* and *Daphnia lumholtzi*) (H. MacIsaac, pers. comm.). Researchers predicted that two NIS zooplankton

species, *C. pengoi* (already present in Lake Ontario) and *D. lumholtzi* (inhabiting reservoirs in Ohio and Michigan in 2000) were likely to invade Lake Erie (Lake Erie LaMP 2000). In August 2001, both species were abundant in the western basin of Lake Erie near the inflow of the Detroit River (H. MacIsaac, pers. comm.). The presence of *C. pengoi* (the fishhook waterflea) represents a significant range expansion, suggesting that the most likely vector for this species is ballast water discharge (H. MacIsaac, pers. comm.). *C. pengoi* reproduces parthenogenically, enabling it to establish quickly, and because of its large size (females, 11–12 mm; males, 7 mm), it will probably reduce both phytoplankton and zooplankton populations and could also compete with young-of-the-year fish for prey. It may also cause major fouling problems on commercial and sport fish lines and nets.

Daphnia lumholtzi, native to Australia, Africa and southwest Asia, is thought to have arrived in reservoirs in the United States when the Nile perch was introduced in Texas to enhance the sport fishery (J. Havel, pers. comm.). Muzinic (2000) published the first record of *D. lumholtzi* in the Great Lakes after he collected specimens from East Harbour State Park, Lakeside, Ohio (western Lake Erie) in 1999. The invasion of this species in the western basin was predicted because of this basin's large surface area and high (25°C) summer water temperatures and a resident zooplankton community dominated by similarly sized invertebrate species (Havel and Hebert 1993; MacIsaac 1999). *Daphnia lumholtzi* is predicted to become a successful invader because of its ability to avoid predation (Goulden et al. 1995).

Degradation of Fish Populations

Fish communities play an important role in determining the overall health of the Lake Erie ecosystem. One hundred and forty-three fish species are present in the Lake Erie basin (USFWS 1995) while 95 species are present in Lake Erie itself (Cudmore 1999). Thirty-four species (24%) of fish in Lake Erie proper are nonindigenous and 19 of these

(56%) are considered established in the Lake Erie basin with the remainder (15 species) having been reported in the basin (Lake Erie LaMP 2000). Non-indigenous invasive fish species comprise approximately 40% of Ontario commercial fish landings (which originate mainly from Lake Erie's commercial fishery) over the past three years (T. Johnson, pers. comm.).

Forage fish provide the link between the zooplankton/benthic communities and fish in the higher trophic levels. Traditionally in Lake Erie, lake herring (Coregonus artedi), sculpins, emerald and spottail shiners made up the bulk of the forage fish community. Lake herring and sculpins are now very rare. Spoonhead sculpin (Cottus ricei), slimy sculpin (Cottus cognatus) and possibly deepwater sculpin (Myoxocephalus thompsoni) were resident in eastern Lake Erie but have not been observed in recent years (Ryan et al. 1999). Over time these species have been replaced by non-native species such as alewife, rainbow smelt, gizzard shad (Dorosoma cepedianum) and round gobies. The smelt fishery is now collapsing due to the decline in Diporeia hoyi (a deepwater amphipod) biomass in the eastern basin and declining productivity (Dermott and Kerec 1997). The cause of Diporeia's disappearance in Lake Erie is still unknown and possible linkages between Diporeia declines and increasing dreissenid populations are being examined (Dermott and Kerec 1997; Nalepa et al. 1999).

Corkum et al. (2001), using data compiled from Baldwin et al. (1979) and annual agency reports submitted to the Great Lakes Fishery Commission, showed that since 1960, NIS represent the major component of the commercial fish harvest. Moreover, in the last century changes have also been reported in the patterns of trophic guilds between commercial landings of native and NIS species from Lake Erie. From 1900 to 1950, piscivores, planktivores, and to a lesser extent omnivores, comprised native landings while benthivores were present in very low numbers (Corkum et al. 2001). The general trend has been a decline in all trophic communities of native fish with omnivores and piscivores now dominating native landings. Since the mid-1920s, native planktivorous fish species have declined while NIS planktivores have increased (Corkum et al. 2001). Prior to 1950, benthivores (e.g., carp and goldfish) represented NIS landings but currently planktivores (e.g., rainbow smelt) dominate the NIS catch, with ominivores and benthivores also very common (Corkum et al. 2001). Changes in feeding guilds resulted from a combination of species invasions, reductions in nutrient concentrations in Lake Erie, and changes in the commercial fishery (i.e., a shift in fishing effort

from higher to lower-valued fishes as preferred species decline in abundance). For example, overfishing reduced lake herring, a native planktivore, but the presence of NIS rainbow smelt and alewife, which feed on larval fish, kept lake herring from recovering (Ryan et al. 1999).

Recent Nonindigenous Fish Species Found in Lake Erie

Nonindigenous fishes found recently in Lake Erie include: the round goby. found in the western basin in 1993 (Jude et al. 1995); threespine stickleback (*Gasterosteus aculeatus*), found in the eastern basin in 1988 (T. Johnson, pers. comm.); tubenose goby, first found in 1996 (Corkum 2000) and occurring locally (e.g., St. Clair River, Detroit River and a few localized nearshore sites in Lake Erie, throughout St. Clair River, Lake St. Clair, Detroit River and western Lake Erie corridor); rudd (*Scardinius erythrophthalmus*), reported in the eastern basin at Crystal Beach, Ontario, in 1997 (Ontario Ministry of Natural Resources 1998); and ghost shiner (*Notropis buchanani*) reported in 1997 (Leach 2001). In 2000, there were unusual sightings of two NIS fish species, Chinese bighead carp (*Hypophthalmichthys nobilis*), west of Point Pelee in the western basin (T. Johnson, pers. comm.), and European flounder (*Platichthys flesus*).

The Chinese bighead carp is native to eastern China and the Lake Erie sighting was probably the result of a fish escape from aquaculture ponds in an adjacent watershed. This species is a filter feeder and if established, it may compete with native fishes for plankton. The European flounder is not a direct threat to native fishes because it is a marine fish and is unable to reproduce in fresh water (Corkum and Austen 2001).

Round Goby

One of the NIS fish species of increasing concern in Lake Erie is the recently established round goby. This species first arrived in Lake Erie in 1993 and is now present in all of the Great Lakes (Leach 2001). In 1996 the Lake Erie round goby population increased by two orders of magnitude. By 1997/1998, round gobies were established in the western basin and western portions of the eastern basin. In 1999, gobies were widespread in Lake Erie with the abundance apparently higher in the central basin (densities of 0–8000 gobies/ha), probably due to the higher percentage of rocky substrate in this basin relative to the western basin (Lake Erie Forage Task Group 2001). Bottom trawls underestimate the species' true abundance because gobies prefer rocky habitat, which is difficult to sample. Eastern basin populations may be equal or higher than the central basin in the future due to the abundance of rocky substrate and dreissenids in the eastern basin (Lake Erie Forage Task Group 2001). Goby populations continue to increase in range and abundance in the eastern basin, while in other areas of Lake Erie, goby abundances remain the same or have decreased relative to 1999 (Lake Erie Forage Task Group 2001).

Major concerns regarding the increase in distribution and abundance of round goby in Lake Erie and other Great Lakes are their ability to transfer contaminants through the food web; their effect on native species (Jude et al. 1995; Dubs and Corkum 1996); their ability to proliferate owing to their multiple spawning habits (Corkum et al. 1998; Wickett and Corkum 1998); and their ability to outcompete mottled sculpins (*Cottus bairdi*) for food resources (small gobies), space (medium-sized gobies) and spawning sites (large gobies), thereby, decimating mottled sculpin populations (Jude et al. 1995; Janssen and Jude 2001; Jude 2001). Round gobies could also interfere with reproductive behaviors of other fishes; for example they have been reported to feed on eggs of lake trout (Chotkowski and Marsden 1999) and lake sturgeon (Nichols et al. 1999), and are thought to feed on eggs and/or larvae of greenside darter (*Etheostoma blennoides*) because this species has declined in areas of overlap with round gobies near Gibralter Island and other similar sites in Lake Erie (Jude 2001). The arrival of gobies may also indirectly affect unionids as sculpins and darters (which may be outcompeted by gobies) are important host fish for unionids (Watters 1995). There are also concerns about the economic implications for commercial fishers of goby bycatch in nets and about the possible release of gobies to new areas through bait bucket transfer by anglers (Charlebois et al. 2001; Jude 2001).

Dreissenids (zebra and quagga mussels) comprise a large part of the diet of adult round gobies (French and Jude 2001). Round gobies may transfer energy and contaminants from benthos into the pelagic zone (Morrison et al. 2000; Jude 2001), thereby contributing to changes in the food web and community structure of Lake Erie. The round goby

is an important prey item of smallmouth bass and was found in the diets of all piscivorous fishes examined in 2000, although importance varied with species (Lake Erie Forage Task Group 2001). Benthic fish (e.g., catfish, smallmouth bass) showed a stronger dependency on round gobies than pelagic species (e.g., walleye and white bass) (Lake Erie Forage Task Group 2001). Gobies are now common in the stomachs of yellow perch, smallmouth bass, white bass, freshwater drum, catfish and walleye (Lake Erie Forage Task Group 2001). Preliminary results from a study evaluating predation by largemouth bass (*Micropterus salmoides*) on round gobies in 15-minute trials show that largemouth bass usually select the largest of three size classes of round gobies (Diers et al. 2001). Other fauna, including mudpuppies and Lake Erie water snakes, also eat gobies (R. Haas, pers. comm. in Jude 2001; King et al. 1999).

Clearly, the round goby will be influential in transferring energy from the lake bottom up through the food chain. However, it is difficult to predict the potential impacts of the round goby because literature from its native range (Black and Caspian seas and associated waters) and invaded areas is limited (Charlebois et al. 2001).

Round gobies are also known to carry botulism Type E toxin (W. Stone, pers. comm.) and may be connected to recent botulism outbreaks in Lake Erie. Significant numbers of fish-eating birds have died in each basin of Lake Erie since 1999 and these die-offs have been linked to *Clostridium botulinum* outbreaks (Domske and Obert 2001; J. Robinson, pers. comm.). Large numbers of birds have been affected including several thousand waterbirds, largely red-breasted mergansers, in the western basin in the fall of 1999; many ring-billed gulls and other gull species in the late summer and fall of 2000 near Eagle, Ontario; hundreds of common loons and possibly thousands of red-breasted mergansers along New York shoreline in December 2000; and 300–500 common loons east of Port Dover on the Ontario shoreline in the late fall of 2001 (Jeff Robinson, pers. comm.; LaMP 2002). Most of the waterbirds affected are migrants moving through the Great Lakes Basin during fall migration.

Many of these bird die-offs have been associated with die-offs of bottom-dwelling fishes (e.g., freshwater drum, *Aplodinotus grunniens*; round gobies) and in some cases a bottom-dwelling amphibian (mudpuppy, *Necturus maculosus*). Botulism-infected birds in Lake Erie had a higher incidence of round gobies in their guts compared with uninfected birds (D. Campbell, pers. comm.). Ward Stone (pers. comm.) has identified botulism Type E in freshwater drum, smallmouth bass and round gobies (retrieved from the guts of smallmouth bass). Fish either float to the water surface and drift shoreward or, in the case of round gobies that lack swim bladders, litter the lake bottom or are washed up on the beaches, enabling birds to feed on fishes harbouring the anaerobic bacteria that contain the toxin. The mechanism for triggering the bacterium, which occurs naturally in the Lake, is still unknown (Domske and Obert 2001).

Degradation of Benthos

Dreissenid invasions in Lake Erie have had marked effects on the Lake Erie ecosystem including loss of energy from the pelagic community to the benthic community; increased water clarity and light penetration in many nearshore and some offshore areas resulting in increased growth of aquatic macrophytes and a decline in habitat availability for walleye; and contaminant uptake and bioaccumulation in the food web (Dahl et al. 1995; Morrison et al. 1995; MacIsaac 1996; Jentes 1999). Moreover, dreissenids change many habitat features on the bottom of Lake Erie and appear to have changed the spatial distributions of some migratory bird species. For example, greater scaup and lesser scaup use dreissenid mussels as a food source and now appear to be more widely distributed on the lake, instead of being found in isolated congregations as was the case prior to the dreissenid invasion (Lambert et al. 2001).

Quagga mussels have recently invaded Lake Erie and are displacing the zebra mussel in the eastern and western basins of Lake Erie, while in the central basin both dreissenids are at similar abundance levels (Dermott and Kerec 1997; R. Dermot, pers. comm.; D. Cuiver, pers. comm.). As a result of their feeding activity and abundance, little unconsumed organic matter would remain to settle on the mud surface for consumption by other deep-water bottom fauna. This has resulted in intense competition for settling material and is having a significant impact on food-web dynamics in deeper portions of Lake Erie. The lack of available settling organic matter may be responsible, in part, for the declines in burrowing amphipods, *Diporeia hoyi* (which feeds extensively on settling diatoms), and native sphaerid (e.g.,

Pisidium) clams (Dermott and Kerec 1997). In the profundal region of eastern Lake Erie, Diporeia hoyi density declined 88% from 1979 to 1993 (after Dreissena polymorpha and D. bugensis became established) and there was an inverse relationship between numbers of Diporeia and Dreissena spp. in individual samples (Dermott and Kerec 1997). Diporeia hoyi in the eastern basin have declined dramatically and rapidly owing to interspecific competition with Dreissena bugensis (Dermott and Munawar 1993). Dreissenids may also reduce diatom numbers, which are a major food item for Diporeia. The fact that Diporeia declined in the eastern basin of Lake Erie suggests that the deep waters of this basin are impaired (J. Ciborowski, pers. comm.). Research is still underway to find the mechanism and/or relationship between declines/loss of Diporeia and dreissenid distribution and abundance (T. Nalepa, pers. comm.). Relationships between dreissenids and Diporeia do not appear straight forward as Diporeia does occur in some areas of Lake Michigan where dreissenids are abundant and Diporeia has been shown to survive translocation from areas with dense populations of Diporeia to areas lacking Diporeia in southern Lake Huron (T. Nalepa, pers. comm.). Another factor that may be associated with declines in diatoms and Diporeia is ozone depletion, which affects UVB radiation (Williamson et al. 2001).

Dreissenids first invaded North America in Lake St. Clair in 1986 (Hebert et al. 1989). Consequently, the impacts of infestation on unionids have been the longest (ca. 14 years) in Lake St. Clair and the Detroit River than elsewhere in North America. Surveys in the lower Detroit River by Schloesser et al. (1998) showed that individuals of all species of all unionid subfamilies declined between 1982–1992/1994 and higher proportions of uncommon than common unionid species were extirpated. In the Detroit River, studies showed that less than 10% of the total unionid population survived 8 years of infestation by zebra mussels (Schloesser et al. 1998). A survey of the upper Detroit River in 1997–1998, using three search methods, found a total of five live unionids of five species, which compares with more than 1000 individuals (26 species) found in the River between 1987–1992 (Schloesser et al. 1998; Schloesser et al. in preparation). These data show a marked decline (95% reduction in number) in native unionids corresponding with increasing numbers and abundance of dreissenids in the Detroit River (Schloesser et al. in preparation). Extant populations of native unionids were virtually extirpated in the western basin of Lake Erie by 1991 (Schloesser et al. 1996). Schloesser and Masteller (1999) found a consistent decline in native unionid populations between 1990 (initial colonization of zebra mussels) and 1996 in Presque Isle Bay on the south shore of Lake Erie; 1990–1991 collections contained about 500 unionids of 15 species with collections in 1994 and 1995 having only three individuals of different species and no individuals observed, respectively (Shloesser and Masteller 1999). Some remnant unionid individuals still occur in the open waters of Lake Erie but their body condition is deteriorating (Haag et al. 1993).

Despite these losses, various native unionid refugia (sites where unionids appear to survive in the presence of dreissenid mussel colonization) have been found in the nearshore waters (small bays, wave swept shores and wetlands) of Lake Erie, particularly in the western basin (Nichols and Wilcox 1997; Schloesser et al. 1997) and the St. Clair delta (Zanatta et al. 2002), together with many of the rivers and streams in the drainage basin (Metcalfe-Smith et al. 1998a). Refuge sites on Lake Erie include the Raisin River mouth (Schloesser et al. 1997), Metzger Marsh (Nichols and Wilcox 1997), Thompson Bay in the outer bay of Presque Isle Bay (E.C. Masteller, pers. comm.), and Lake St. Clair (Zanatta et al. 2002). Recent surveys from 1998–2001 in Lake St. delta show unionid refuges to occur in shallow (<1–2 m deep) sites exhibiting high connectivity to Lake St. Clair, presumably with wave action, ice scouring, and changing water levels encouraging zebra mussel release from the substrate (Zanatta et al. 2002). Metzger Marsh and St. Clair delta provide refuges for 20 (Nichols and Amberg 1999) and 22 (Zanatta et al. 2002) species of native unionids, including several rare species. These two sites may support the richest remnant communities of unionids (post-zebra mussel invasion) of the lower Great Lakes (Zanatta et al. 2002); sites near Metzger marsh, Bass Island, the southwest shore of Lake Erie, the Detroit River and Rondeau Bay on the north side of Lake Erie were largely devoid of native unionids based on recent surveys (Zanatta et al. 2002).

Tributaries on the north side of Lake Erie (including Lake St. Clair) continue to act as "refugia" for native unionids. However, the introduction of zebra mussels to reservoirs on the Grand River, ON, could quickly decimate native

unionid populations. Unionids have declined in lakes and tributaries in the Great Lakes Basin and elsewhere in North America due to habitat destruction from dams, channel modification, siltation, and introduction of nonindigenous molluscs. Freshwater mussels are threatened by disturbances impacting them directly, and those that affect their host fish populations (larval stage is an obligate ectoparasite on fish and often host specific) (Bogan 1993). The Nature Conservancy recognizes 55% of the mussel fauna as imperiled (Master 1990); no other widespread animal group is known to approach this level of faunal collapse (Metcalfe-Smith et al. 1998b). Therefore, conservation measures are needed to protect and manage sites with native unionids to ensure the survival and viability of these populations. Introduction of zebra mussels into reservoirs on Lake Erie tributaries must be prevented. Reservoirs with retention times greater than 20–30 days allow veligers to develop and settle, after which impounded populations seed downstream reaches on an annual basis (Metcalfe-Smith et al. 2000). Nine out of 35 native unionid species occurring in the Canadian waters of the lower Great Lakes drainage basin were ranked as highly vulnerable to zebra mussels (Metcalfe-Smith et al. 1998b). Species that occur mainly in the Great Lakes themselves, or in lower reaches of larger tributaries, are most at risk from impacts of zebra mussels while headwater species are unlikely to encounter zebra mussels throughout most of their range (Metcalfe-Smith et al. 1998b).

The Lake Erie and Lake St. Clair drainages are home to the richest mussel fauna in Canada (Metcalfe-Smith et al. 1998a). The top four tributaries in Lake Erie in terms of mussel diversity include the St. Joseph River in Indiana with 35 live species (Watters 1998); the Sydenham River, Ontario with 34 live species (J. Metcalfe-Smith, pers. comm.); the Clinton River, Michigan with 26 live species (Strayer 1980); and the Grand River with 25 live species in 1995/1997–98 (Metcalfe-Smith et al. 2000). Five species native to the Sydenham River are endangered in Canada: snuffbox (Epioblasma triquetra), salamander mussel (Simpsonaias ambigua), wavy-rayed lampmussel (Lampsilis fasciola) (now extirpated in the Sydenham River), rayed bean (Villosa fabalis) (now restricted to the Sydenham River, and northern riffleshell (Epioblasma torulosa rangiana) (Sydenham River population is one of only three populations in North America showing evidence of successful reproduction) (Staton et al. 2000).

The northern riffleshell, which is endangered in Canada and the United States, could become extinct within this decade if conservation measures aren't enacted; it is presumed to be eradicated from Lake Erie, Lake St. Clair, and the Huron-Erie corridor due to the invasion of these areas by the zebra mussel (Staton et al. 2000). Populations of northern riffleshell in the Sydenham and Ausable rivers are not at significant risk of exposure to zebra mussels because these rivers are not regulated due to their low gradient; consequently there are no reservoirs that could permanently support dreissenids if they were introduced (Staton et al. 2000). Allen and Ramcharan (2001) showed that permanent zebra mussel populations are most likely to establish in waterways with moderate ionic strength and which also have some impoundment areas to increase long-term population persistence. However, the presence of zebra mussels throughout the Great Lakes precludes the recovery of the northern riffleshell throughout much of its original range. Comparisons with historical data suggest that the abundance of this species may have declined by as much as 90% over the past three decades (Staton et al. 2000).

In some tributary reaches, such as the lower reaches of the Grand River, Ontario, native unionid species richness has increased; this increase has been attributed to improved water quality over the last 25 years (Metcalfe- Smith et al. 2000). Burrowing mayflies are now recovering in many areas of Lake Erie and their recovery is being attributed to significant improvements in water and sediment quality. Mayflies (*Hexagenia* spp.) are an important traditional food resource for many fish species and transfer energy from the benthic community to the pelagic community. *Hexagenia* mayflies were widely distributed (80% of sites) and abundant (ca. 160 nymphs/m2) in the western basin of Lake Erie in 1929–1930 (Schloesser et al. 2001). Mayfly larval densities declined in the 1930s, bottomed out in the 1960s, and remained at low levels through to 1990. In the 1990s, densities increased dramatically so that by 1997, mayflies met a mayfly-density management goal (ca. 350 nymphs/m² — similar to those of the 1930s and 1950s) based on pollution-abatement programs (Schloesser et al. 2001). Between 1996–1999 mayfly emergences were similar to those in the 1930s. The factors contributing to mayfly recolonization are uncertain but pollution-abatement programs,

explosive growth of zebra mussels, which diverted plankton foods to bottom substrates, and the attainment of high enough densities nearshore to supply a sufficient number of recruits to offshore waters may all have contributed to recolonization (Krieger et al. 1996; Schloesser et al. 2001). High densities of mayflies are found in the extreme western section of Lake Erie. Adult emergences have occurred along the entire south shore of Lake Erie in the United States and at Rondeau, Long Point, and Port Dover on the Canadian side. Studies in Lake St. Clair and Lake Erie in 1997–1999 indicate that mayfly recruitment success is variable between and within years and, therefore, caution should be exercised when interpreting fluctuations in mayfly densities. Mayfly densities affect other organisms, particularly the pelagic component of the food web. For example, growth rates of yellow perch are controlled in part by the abundance of *Hexagenia*, with mayflies comprising up to 50% (on a volume basis) of both adult and juvenile perch diet at certain time periods between 1994–1996 (M. Bur, pers. comm. cited in Madenjian et al. 1998).

Potential Invaders of Lake Erie

Species that are most likely to invade Lake Erie include species living in freshwater systems in temperate climates; estuarine (brackish water) species from foreign ports that can tolerate fresh water (Witt et al. 1997); or species living in nearby drainages. Alterations in the thermal regime and ice cover of Lake Erie (and other Great Lakes) related to climate change will affect habitat suitability and the ability of nonindigenous invasive species to become established in the basin. Additional NIS introductions to Lake Erie will cause more changes in the ecosystem and even less predictability. Twenty-five species have been identified as possible invaders to the Great Lakes (Grigorovich et al. this volume). Some potential future aquatic invaders to Lake Erie include European water chestnut (*Trapa natans*) a nuisance aquatic weed presently found in New York on the south shore of Lake Ontario, and in Pennsylvania; *Hydrilla verticillata*, a submergent plant which is a problem in Florida; blueback herring (*Alosa aestivalis*); fourspine stickleback (*Apeltes quadracus*) (T. Johnson, pers. comm.); and Eurasian ruffe (*Gymnocephalus cernuus*) which is predicted to enter Lake Erie within the next five years and will likely compete with yellow perch and walleye for food (Mayo et al. 1998).

Management Implications

Pimentel (2000) showed that more than 50 000 invasive species occur in the United States. These species are estimated to cost US\$137 billion annually in direct losses, damages and control costs, along with indirect costs, in a range of sectors from natural resources to human health.

Nonindigenous species are a key factor influencing change in lake ecosystems. Invasion corridors still exist both within the Great Lakes and between the Great Lakes and other areas such as the Ponto-Caspian region. Risk assessments of potential invaders are needed together with regulatory controls on various vectors. Prevention is the most effective action because once species such as zebra mussels and round gobies become established they are virtually impossible to eradicate. Furthermore, one species often supports the establishment of another NIS. For example, the abundance of zebra and quagga mussels in Lake Erie, together with the round goby's multiple spawning habits, has hastened the establishment and spread of the round goby in Lake Erie and other Great Lakes (Ray and Corkum 1997; Jude 2001).

Research and management measures need to be taken with regard to the efficacy of ballast water management (for both ballast on board and no ballast on board vessels); other ship-mediated NIS transfer mechanisms (e.g., hull fouling); the food industry; the pet trade; aquaculture; horticulture; and fish-stocking. Effective regulations and consistency in regulations and policies across jurisdictions, wherever possible, are necessary to help prevent, control, and eradicate invasive species transported into the Great Lakes. Ballast water is a major vector for NIS introductions into the Great Lakes with no ballast on board vessels (NOBOBs) potentially contributing many new NIS, particularly invertebrates, into aquatic ecosystems. Aquarium and water garden fish introductions are a global problem and an important vector for NIS introductions. Although one in every four fish species introductions in the US results from the aquarium trade, little effort is directed toward public awareness of aquarium releases in the Great Lakes basin (Dextrase and Paleczny 2000). Of nine fish species associated with aquarium and water garden releases in Ontario, three species have been reported in Lake Erie [goldfish (Carassius auratus), pacu (Colossoma sp.) and suckermouth catfish (Panaque

sp.)] (Dextrase and Paleczny 2000). In July 2001, a suckermouth catfish (*Lyposarcus pardalis*) originating from South America was also caught in Lake Erie demonstrating that release of aquarium fish is an ongoing problem (A. Dextrase, pers. comm.). Anglers continue to dump bait buckets in lakes and rivers, risking the introduction of round gobies and other NIS into inland waters (Dextrase and Mackay 1999) and most sportfishing regulations do not adequately address the use and transportation of baitfish (Litvak and Mandrak 1993). Litvak and Mandrak (1993) identify some options that could be implemented to mitigate ecosystem damage from the harvest and use of baitfish.

The Province of Ontario and eight states bordering on the Great Lakes all have some restrictions on NIS, but policies are inconsistent. The Lake Erie Lakewide Management Plan (http://www.on.ec.gc.ca/glimr/lakes/erie/http://www.epa.gov/glnpo/lakeerie), a binational program (Canada/United States of America) aimed at restoring the biological, chemical and physical integrity of Lake Erie, will also address the role of NIS in the Lake Erie ecosystem and propose actions that can be taken to control or restrict further NIS introductions. Recently, a draft document has been prepared for a Canadian "National Policy/Code on Introductions and Transfers of Aquatic Organism" that will apply to all intentional introductions for stocking or aquaculture. On 5–7 November 2001, Environment Canada organized a "National Workshop on Invasive Alien Species" to:

- identify and clarify fundamental issues in the management of invasive alien species in Canada;
- · develop a draft framework for a national plan that identifies key policy and management options; and
- outline a process to develop a draft Canada-wide plan for the fall of 2002.

Several agreements, policies, and management guidelines outline the need to address the continuing influx of nonindigenous invasive species to the Great Lakes Basin and other ecosystems including:

- Article 8H of the Convention on Biological Diversity calls upon Parties to "prevent the introduction, control or
 eradicate those alien species which threaten ecosystems, habitats or species." Interim guiding principles and
 recommendations were produced in the Convention for implementing Article 8H.
- the United States National Invasive Species Council Management Plan in the United States and the National Strategy on Alien Invasive Species in Canada (under development, M. Hovorka, pers. comm.) will address prevention, early detection and rapid response, control and management, restoration, research, education information management, international cooperation, and leadership and coordination issues.
- the Great Lakes Action Plan for Aquatic Nuisance Species Prevention and Control, an agreement recently signed by the Great Lakes–St. Lawrence Governors and Premiers to ensure a regional approach to preventing and controlling aquatic nuisance species. This plan will include a Ballast Water Management Policy to address the introduction and spread of aquatic nuisance species.

The development and implementation of effective management plans for biological invaders in Lake Erie, and throughout the Great Lakes basin, is needed to prevent additional invasions and control existing NIS in these aquatic ecosystems.

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Literature Cited

Allen, Y.C.; Ramcharan, C.W. 2001. Dreissena distribution in commercial waterways of the US: using failed invasions to identify limiting factors. Canadian Journal of Fisheries and Aquatic Sciences 58:898–907.

Bogan, A.E. 1993. Freshwater bivalve extinctions (Mollusca: Unionidae): a search for causes. American Zoologist 33:599–609.

Budd, J.W.; Beeton, A.M.; Stumpf, R.P.; Culver, D.A.; Kerfoot, W.C. 2001. Satellite observations of *Microcystis* blooms in western Lake Erie and Saginaw Bay, Lake Huron. Verh. Int. Ver. Limnol. 27:3787–3793.

Charlebois, P.M.; Corkum, L.D.; Jude, D.J.; Knight, C. 2001. The round goby (*Neogobius melanostomus*) invasion: current research and future needs. Journal of Great Lakes Research 27:263–266.

Chotkowski, M.; Marsden, J.E. 1999. Round goby and mottled sculpin predation on lake trout eggs and fry: field predictions from laboratory experiments. Journal of Great Lakes Research 25:26–35.

Corkum, L.D. 2000. Non-indigenous invasive species in Lake Erie. Pages 11–13 in J. Letterhos, ed. Lake Erie Lakewide Management Plan (LaMP) 2000. Prepared by the Lake Erie LaMP Work Group under the direction of the Lake Erie LaMP Management Committee. Environment Canada, Ontario Region and US Environmental Protection Agency, Region 5. Burlington, ON. On-line: http://www.epa.gov/glnpo/lakeerie/lamp2000/index.html

Corkum, L.D.; Austen, M. 2001. Biological invasions in the Lake Erie ecosystem. *In* J.J.H. Ciborowski; M.N. Charlton; R.G. Kreis; J.P. Reuter, eds. Lake Erie at the Millenium: Changes, Trends and Trajectories. Canadian Scholars' Press Inc., Toronto, ON.

Corkum, L.D.; MacInnis, A.J.; Wickett, R.G. 1998. Reproductive habits of round gobies. Great Lakes Research Review 3:13–20.

Corkum, L.D.; Mills, E.L.; Leach, J.H.; Johnson, T.B. 2001. Lake Erie — a history of fish invasions and trophic trends for the future. *In*: J.J.H. Ciborowski; M.N. Charlton; R.G. Kreis; J.P. Reuter, eds. Lake Erie at the Millennium: Changes, Trends and Trajectories. Canadian Scholars' Press Inc, Toronto, ON.

Cudmore, B.C. 1999. Changing biodiversity and the theory of resistance to invasion: the fishes of the Laurentian Great Lakes as a case study. M.Sc. thesis, University of Toronto, Toronto, ON.

Dahl, J.A.; Graham, D.M.; Dermott, R.; Johannsson, O.E.; Millard, E.S.; Miles, D.D. 1995. Lake Erie 1993, western, west central and eastern basins: changes in trophic status, and assessment of the abundance, biomass and production of the lower trophic levels. Canadian Technical Report of Fisheries and Aquatic Sciences. No. 2070. 118 pp.

Dermott, R.; Kerec, D. 1997. Changes in the deepwater benthos of eastern Lake Erie since the invasion of *Dreissena*: 1979–1993. Canadian Journal of Fisheries and Aquatic Sciences 54:922–930.

Dermott, R.; Munawar, M. 1993. Invasion of Lake Erie offshore sediments by *Dreissena*, and its ecological implications. Canadian Journal of Fisheries and Aquatic Sciences 50: 2298–2304.

Dextrase, A.; Mackay, B. 1999. Evaluating the effectiveness of ANS outreach materials (Abstract). Page 172 in Proceedings of the 9th International Zebra Mussel and Aquatic Nuisance Species Conference, Duluth, MN 26–30 April 1999. The Professional Edge, Pembroke, ON.

Dextrase, A.; Paleczny, E. 2000. Public outreach efforts to reduce the risk of aquarium fish introductions. Page 402 in Proceedings of the 10th International Aquatic Nuisance Species and Zebra Mussel Conference, Toronto, ON, 13–17 February 2000. The Professional Edge, Pembroke, ON.

Diers, J.; Fynn-Aikins, K; Diggins, T. 2001. Experimental analysis of native sport fish predation on the round goby (*Neogobius melanostomus*). Abstracts of the International Association of Great Lakes Annual Conference 2001.

Domske, H.M.; Obert, E.C. 2001. Avian botulism in Lake Erie. Workshop Proceedings, New York Sea Grant and Pennsylvania Sea Grant, Erie, PA, 24–25 January 2001.

http://www.pserie.psu.edu/seagrant/extension/Avian_Botulism_Workshop.pdf

Dubs, D.O.; Corkum, L.D. 1996. Behavioral interaction between round gobies (*Neogobius melanostomus*) and mottled sculpins (*Cottus bairdii*). Journal of Great Lakes Research 22:838–845.

French, J.R.P.; Jude, D.J. 2001. Diets and diet overlap of nonindigenous gobies and small benthic native fishes co-inhabiting the St. Clair River, Michigan. Journal of Great Lakes Research 27:300-311.

Goulden, C.L.; Tomljanovich, D.; Kreeger, D.; Corney, E. 1995. The invasion of *Daphnia lumholtzi* Sars (Cladocera, Daphniidae) into a North American reservoir. Pages 9-38 in S.W. Hamilton; D.S. White; E.W. Chester; A.F. Scott, eds. 1995. Proceedings of the sixth symposium on the natural history of the lower Tennessee and Cumberland River Valleys. The Center for Field Biology, Austin Peay State University, Clarksville, Tennessee.

Grigorovich, I.A.; Colautti, R.I.; MacIsaac, H.J. (this volume). Invasion hotspots of the Laurentian Great Lakes. P. 188. Proceedings of the 11th International Conference on Aquatic Invasive Species, February 25-March 1, 2002. Alexandria, Virginia.

Haag, W.R.; Berg, D.J.; Garton, D.W.; Farris, J.L. 1993. Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (*Dreissena polymorpha*) in western Lake Erie. Canadian Journal of Fisheries and Aquatic Sciences 50:13-19.

Hall, S.R.; Mills, E.L. 2000. Exotic species in large lakes of the world. Aquatic and Ecosystem Health Management 3:105-135.

Havel, J.E.; Hebert, P.D.N. 1993. *Daphnia lumholtzi* in North America: another exotic zooplankter. Limnology and Oceanography 38:1837-1841.

Hebert, P.D.N.; Muncaster, B.W.; Mackie, G.L. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 46:1587-1591.

International Joint Commission. 1994. Revised Great Lakes Water Quality Agreement of 1978. International Joint Commission. February, 1994. 64 pp.

Janssen, J.; Jude, D.J. 2001. Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbour, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. Journal of Great Lakes Research 27:319-328.

Jentes, J. 1999. Zebra mussels: Key to contaminant cycling. In Twineline, Vol 21, No. 4. Ohio Sea Grant College Program, The Ohio State University, Columbus, OH.

Jude, D.J. 2001. Round and tubenose gobies: 10 years with the latest Great Lakes phantom menace. Dreissena 11:1-14.

Jude, D.J.; Janssen, J.; Crawford, G. 1995. Ecology, distribution, and impact of the newly introduced round and tubenose gobies on the biota of the St. Clair and Detroit Rivers. Pages 447-460 in M. Munawar; T. Edsall; J. Leach, eds. The Lake Huron Ecosystem: Ecology, Fisheries and Management. SPB Academic Publishing, Amsterdam.

King, R.B.; Qureal-Regil, A.; Bittner, T.D.; Kerfin, J.M. 1999. Nerodia sipedon insularum (Lake Erie water snake) diet. Herpetological Review 30:169-170.

Krieger, K.A.; Schloesser, D.W.; Manny, B.A.; Trisler, C.E.; Heady, S.E.; Ciborowski, J.J.H.; Muth, K.M. 1996. Recovery of burrowing mayflies (Ephemeroptera: Ephemeridae: *Hexagenia*) in western Lake Erie. Journal of Great Lakes Research 22:254-263.

Lake Erie Forage Task Group. 2001. Report of the Lake Erie Forage Task Group. March, 2001.

Lake Erie LaMP 2000. The lakewide management report. Prepared by the Lake Erie LaMP Work Group under the direction of the Lake Erie LaMP Management Committee. Environment Canada, Ontario Region and U.S.Environmental Protection Agency, Region 5.

Lake Erie LaMP 2002. The lakewide management report. Prepared by the Lake Erie LaMP Work Group under the direction of the Lake Erie LaMP Management Committee. Environment Canada, Ontario Region and U.S. Environmental Protection Agency, Region 5.

Lambert, L.; Robinson, J.; Shieldcastle, M.; Austen, M. 2001. Executive Summary: Degraded Wildlife Populations and Loss of Wildlife Habitat. Technical Report No. 5, Lake Erie Lakewide Management Plan (LaMP) Technical Report Series. Environment Canada and U.S. Environmental Protection Agency, Region 5. September 7, 2001.

Leach, J.H. 2001. Biological invasions of Lake Erie. Point Pelee Natural History News 1:65-73.

Litvak, M.K.; Mandrak, N.E. 1993. Ecology of freshwater baitfish use in Canada and in the United States. Fisheries 18:6-13.

MacIsaac, H.J. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. American Zoologist 36:287-299.

MacIsaac, H.J. 1999. Biological invasions in Lake Erie: past, present and future. Pages 305-322 in M. Munawar, T. Edsall, and I.F. Munawar, eds. State of Lake Erie – Past, Present and Future. Backhuys Publishers, Leiden, The Netherlands.

Madenjian, C.P.; Schloesser, D.W.; Krieger, K.A. 1998. Population models of burrowing mayfly recolonization in western Lake Erie. Ecological Applications 8:1206-1212.

Makarewicz, J.C.; Lewis, T.W.; Bertram, P. 1999. Phytoplankton composition and biomass in the offshore waters of Lake Erie: pre- and post-Dreissena introduction (1983-1993). Journal of Great Lakes Research 25:135-148.

Master, L. 1990. The imperiled status of North American aquatic animals. Biodviersity Network News 3:1-2, 7-8.

Mayo, K.R.; Selgeby, J.H.; McDonald, M.E. 1998. A bioenergetics modeling evaluation of top-down control of ruffe in the St. Louis River, western Lake Superior. Journal of Great Lakes Research 24:329-342.

Metcalfe-Smith, J.L.; Mackie, G.L.; Di Maio, J.; Staton, S.K. 2000. Changes over time in the diversity and distribution of freshwater mussels (Unionidae) in the Grand River, Southwestern Ontario. Journal of Great Lakes Research 26:445-459.

Metcalfe-Smith, J.L.; Staton, S.K.; Mackie, G.L.; Lane, N.M. 1998a. Changes in the biodiversity of freshwater mussels in the Canadian waters of the Lower Great Lakes drainage basin over the past 140 years. Journal of Great Lakes Research 24:845-858.

Metcalfe-Smith, J.L.; Staton, S.K.; Mackie, G.L.; Lane, N.M. 1998b. Selection of candidate species of freshwater mussels (Bivalvia: Unionidae) to be considered for national status designations by COSEWIC. Canadian Field-Naturalist 112:425-440.

Mills, E.L.; Leach, J.H.; Carlton, J.T.; Secor, C.L. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. Journal of Great Lakes Research 19:1-54.

Morrision, H.T.; Whittle, D.M.; Haffner, G.D. 2000. The relative importance of species invasions and sediment disturbance in regulating chemical dynamics in western Lake Erie. Ecological Modeling 125:279-294.

Morrison, H.; Yankovich, T.; Lazar, R.; Haffner, G.D. 1995. Elimination rate constants of 36 PCBs in zebra mussels (*Dreissena polymorpha*) and exposure dynamics in the Lake St. Clair-Lake Erie corridor. Canadian Journal of Fisheries and Aquatic Sciences 52:2574-2582.

Munawar, M.; Munawar, I.F.; Weisse, T.; van Stam, H.; Fitzpatrick, M.; Lorimer, J.; Wenghofer, C.; Carou, S. 1999. Probing microbial food-web structure in Lake Erie. Pages 417-439 in M. Munawar; T. Edsall; I.F. Munawar, eds. State of Lake Erie - Past, Present and Future.. Ecovision World Monograph Series, Backhuys Publishers, Leiden, The Netherlands.

Muzinic, C J. 2000. First record of Daphnia lumholtzi Sars in the Great Lakes. Journal of Great Lakes Research 26:352-354.

Nalepa, T.F.; Hartson, D.J.; Lang, G.L.; Lozano, S.J. 1999. Decline in benthic macroinvertebrate populations in southern Lake Michigan, 1980-1993. Dreissena 9:1-5.

Nichols, S.J.; Amberg, J. 1999. Co-existence of zebra mussels and freshwater unionids: population dynamics of *Leptodea fragilis* in a coastal wetland infested with zebra mussels. Canadian Journal of Zoology 77:423-432.

Nichols, S.J., J. French, G. Kennedy, G. Black, J. Allen and M. McCoy. 1999. Estimating the impact of round gobies on lake sturgeon recruitment (p. 117). 9th International Zebra Mussel & Aquatic Nuisance Species Conference, Duluth, Minnesota, April 26-30, 1999.

Nichols, S.J.; Wilcox, D.A. 1997. Burrowing saves Lake Erie clams. Nature 389:921. Ontario Ministry of Natural Resources. 1998. Rudd in the Great Lakes. Ontario Ministry of Natural Resources Fact Sheet.

Pimentel, D.; Lach, L.; Zuniga, R.; Morrison, D. 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50:53-65.

Ray, W. J.; Corkum, L.D. 1997. Predation effects on zebra mussels by the round goby. Environmental Biology of Fishes 50:267-273.

Ricciardi, A. 2001. Facilitative interactions among aquatic invaders: Is an "invasional meltdown" occurring in the Great Lakes? Canadian Journal of Fisheries and Aquatic Sciences 58:2513-2525.

Ryan, P.A.; Witzel, L.D.; Paine, J.; Freeman, M.; Hardy, M.; Scholten, A.; Sztramko, L.; MacGregor, R. 1999. Recent trends in fish populations in eastern Lake Erie in relation to changing lake trophic state and food web. Pages 241-289 in M. Munawar; T. Edsall; I.F. Munawar, eds. State of Lake Erie - Past, Present and Future.. Ecovision World Monograph Series, Backhuys Publishers, Leiden, The Netherlands.

Schloesser, D.W. In preparation. Extirpation of freshwater Unionids (Bivalvia: Unionidae) in the Detroit River of the Great Lakes.

Schloesser, D.W.; Kovalak, W.P.; Longton, G.D.; Ohnesorg, K.L.; Smithee, R.D. 1998. Impact of zebra and quagga mussels (*Dreissena* spp.) on freshwater unionids (Bivalvia: Unionidae) in the Detroit River of the Great Lakes. American Midland Naturalist 140:299-313.

Schloesser, D.W.; Krieger, K.A.; Ciborowski, J.J.H.; Corkum, L.D. 2001. Recolonization and possible recovery of burrowing mayflies (Ephemeroptera: Epheridae: *Hexagenia* spp.) in Lake Erie of the Laurentian Great Lakes. Journal of Aquatic Ecosystem Stress and Recovery 8:125-141.

Schloesser, D.W.; Masteller, E.C. 1999. Mortality of unionid bivalves (Mollusca) associated with dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*) in Presque Isle Bay, Lake Erie. Northeastern Naturalist 6:341-352.

Schloesser, D.W.; Nalepa, T.F.; Mackie, G.L. 1996. Zebra mussel infestation of unionid bivalves (Unionidae) in North America. American Zoologist 36:300-310.

Schloesser, D.W.; Smithee, R.D.; Longton, G.D.; Kovalak, W.P. 1997. Zebra mussel induced mortality of unionids in firm substrata of western Lake Erie and a habitat for survival. American Malacological Bulletin 14:67-74.

Staton, S.K.; Metcalfe-Smith, J.L.; West, E.L. 2000. Status of the Northern Riffleshell, *Epioblasma torulosa rangiana* (Bivalvia: Unionidae), in Ontario and Canada. Canadian Field-Naturallist 114:224-235.

Steward, T.W.; Miner, J.G.; Lowe, R.L. 1998. Macroinvertebrate communities on hard substrates in western Lake Erie: Structuring effects of *Dreissena*. Journal of Great Lakes Research 24:868-879.

Strayer, D.L.1980. The freshwater mussels (Bivalvia: Unionidae) of the Clinton River, Michigan, with comments on man's impact on the fauna, 1870-1978. The Nautilus 94:142-149.

United States Fish and Wildlife Service (USFWS) 1995. Great Lakes Fishery Resources Restoration Study. Report to Congress. USFWS, Lansing, Michigan.

Vanderploeg, H.A.; Liebig, J.R.; Çarmichael, W.W.; Agy, M.A.; Johengen, T.H.; Fahnenstiel, G.L.; Nalepa, T.F. 2001. Zebra mussel (*Dreissena polymorpha*) selective filtration promoted toxic *Microcystis* blooms in Saginaw Bay (Lake Huron) and Lake Erie. Canaidan Journal of Fisheries and Aquatic Sciences 58:1208-1221.

Watters, G.T. 1995. An annotated bibliography of the reproduction and propagation of the Unionidae (primarily of North America). Ohio Biological Survey Miscellaneous Contributions 1:1-158.

Watters, G.T. 1998. Freshwater mussel survey of the St. Joseph River drainage, exclusive of Fish Creek. Final report to the Indiana Chapter of The Nature Conservancy.

Wickett, R.G.; Corkum, L.D. 1998. You've got to get wet: a case study of the exotic Great Lakes fish, round goby (*Neogobius melanostomus*). Fisheries 23:26-27.

Williams, J.D.; Warren, M.L.,Jr.; Cummings, K.S.; Harris, J.L.; Neves, R.J. 1993. Conservation status of freshwater mussels of the United States and Canada. Fisheries 18:6-22.

Williamson, C.E.; Neale, P.J.; Grad, G.; De Lange, H.J. 2001. Beneficial and detrimental effects of UV on aquatic organisms: implications of spectral variation. Ecological Monographs 11:1843-1857.

Witt, J.D.S.; Hebert, P.D.N.; Morton, W.B. 1997. *Echinogammarus ischnus*: another crustacean invader in the Laurentian Great Lakes basin. Canadian Journal of Fisheries and Aquatic Sciences **5**4:264-268.

Zanatta, D.T.; Mackie, G.L.; Metcalfe-Smith, J.L.; Woolnaugh, D.A. 2002. A refuge for native freshwater mussels (Bivalvia: Unionidae) from impacts of the exotic zebra mussel (*Dreissena polymorpha*) in Lake St. Clair. Journal of Great Lakes Research 3:479-489.