

United States cause approximately \$120 billion per year in economic damage.

The worldwide problem of NIS has intensified with the development of a global economy. Because approximately 98 percent of world trade by weight is transported by sea (Reeves 1999), shipping is a strong vector for the movement of NIS worldwide. For example, shipping has accounted for 38 of 60 unintentional introductions to the Baltic Sea during the past 200 years (Leppäkoski *et al.* 2002). NIS in the Baltic Sea have caused economic damage to fisheries, shipping and industry, and include the hydrozoan *Cordylophora caspia*, the barnacle *Balanus improvisus*, the cladoceran *Cercopagis pengoi*, and the bivalve *Dreissena polymorpha*. In the Ponto-Caspian region, Grigorovich *et al.* (2002) identified 136 free-living and 27 parasitic invertebrate NIS that had established reproducing populations and emphasized that activities related to global trade – both shipping and the construction of canals and reservoirs – provided dispersal opportunities to and within the region. The recent addition of the North American ctenophore *Mnemiopsis leidyi* to the Caspian Sea portends catastrophic ecological and economic shifts in this basin (Shiganova 1998).

The Laurentian Great Lakes (Fig. 6.1), collectively the world's largest freshwater resource, are among the best studied and are well documented with respect to transport vectors and impacts of NIS (Mills *et al.* 1993, 1994; Hall and Mills 2000; Ricciardi 2001). Over 176 (183 reported as of 2007) non-indigenous aquatic plants and animals have been recognized as introduced and established in the Great Lakes basin (Mills *et al.* 1993; Ricciardi 2001, 2006; Nicholls and MacIsaac 2004), and the arrival of most of these species can be linked either directly or indirectly to globalization. Here we discuss how globalization has affected the structure and function of Great Lakes ecosystems, focusing on transoceanic shipping as a primary transport vector of NIS to the Great Lakes. We pay particular attention to five species introduced from the Ponto-Caspian region of Eurasia (Fig. 6.1), an area that has been identified as an important source of NIS to the Great Lakes (Ricciardi and MacIsaac 2000). Also, we discuss the effects these NIS have had – and may have in the future – on Great Lakes fisheries.

HISTORY OF GLOBALIZATION AND BIOLOGICAL INVASIONS IN THE GREAT LAKES

The first human-mediated introductions of NIS to the Great Lakes likely occurred through the activities of native peoples. However, the

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Globalization, biological invasions, and ecosystem changes in North America's Great Lakes

INTRODUCTION

Globalization, in the context of biological invasions, is the increased movement of species around the world. In this chapter, non-indigenous species (NIS) are defined as taxa moved from one geographic location of the world to another from which they were historically absent. The largest geographic barriers to species dispersal, the world's oceans, have been circumvented by the development of a global economy. Increased demand for and transport of goods has resulted in the transfer – both intentional and unintentional – of NIS on unprecedented scales. For example, colonization rates of European crustaceans in North America are estimated to be 50 000 times background levels associated with natural dispersal (Hebert and Cristescu 2002). A number of dispersal vectors are responsible for transport of aquatic NIS, though transoceanic shipping has played a particularly important role as the global economy has expanded.

Establishment of NIS represents one of the most significant threats to the world's indigenous biota (Mooney and Drake 1989; Mack *et al.* 2000), in addition to adverse ecological and economic effects that they impart on lakes throughout the world (e.g., Hall and Mills 2000). For example, establishment of Nile perch (*Lates niloticus*) in Lake Victoria and peacock bass (*Cichla ocellaris*) in Gatun Lake resulted in extirpation or decline of native fish species (Zaret and Paine 1973; Ogunu-Ohwaya 1990; Witte *et al.* 1992). In Lake Titicaca, the introduction of brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) led to a disease outbreak (*Ichthyophthirius multifiliis* or Ich), a short-lived commercial fishery, and competition with native species (Hall and Mills 2000). Pimentel *et al.* (2005) estimated that NIS in the

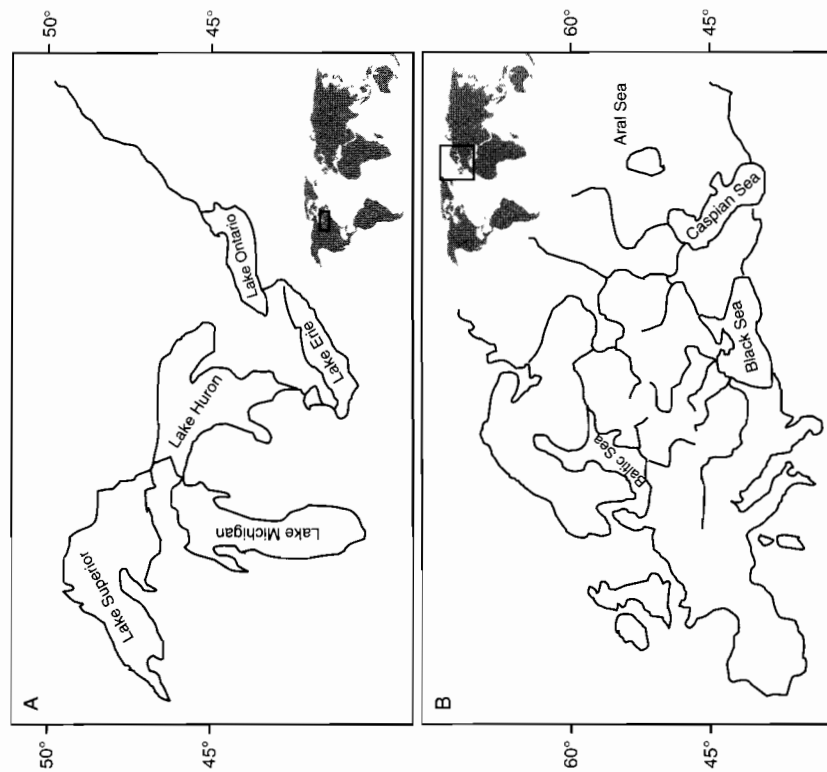


Figure 6.1 The North American Great Lakes (A) and Eurasia (B).

intensification of globalization's effect on the region did not begin until the arrival of European settlers about four centuries ago. The settlers brought animals and plants intentionally for cultivation and unintentionally in ship solid ballast and animal feeds. For example, purple loosestrife (*Lythrum salicaria*) arrived at ports on the Atlantic coast with imported sheep, in solid ballast, or as a cultivated plant (Mills et al. 1993). Three mollusk species (*Valvata piscinalis*, *Pisidium amnicum*, and *Bithynia tentaculata*) of Eurasian origin that were introduced prior to the turn of the twentieth century are believed to have been transported either in the solid ballast of ships or in straw and marsh grass packaging materials used to protect fragile articles during their overseas journey (Mills et al. 1993). During the late nineteenth century and early twentieth century, human population growth and concomitant development of lands surrounding the Great Lakes

resulted in deforestation of the watershed, excessive nutrient loading, and the overharvesting of fishes. The detrimental effects of these large-scale changes on Great Lakes fisheries were amplified by the introduction of NIS via a range of vectors, including deliberate and accidental release, migration through canals, and shipping activities. Shipping vectors transitioned from solid to liquid ballast around the turn of the century, and NIS that established thereafter switched from primarily terrestrial to aquatic-based taxa.

Although some species have entered the Great Lakes from adjacent watersheds or the Atlantic coast, their arrivals are an indirect result of globalization. For example, two fish species that have had profound effects on Great Lakes fisheries, alewife (*Alosa pseudoharengus*) and sea lamprey (*Petromyzon marinus*), gained access to the lakes because of the construction of and improvements to connecting channels (the St. Lawrence Seaway and the Welland Canal), the purpose of which was to provide passage for large ships from the Atlantic Ocean to inland ports. Other species have been introduced intentionally. For example, common carp (*Cyprinus carpio*) was imported as early as 1831 for propagation in a private pond (DeKay 1842), and stocking of these fish in the Great Lakes basin by the U.S. Fish Commission ensued sometime after 1879 (Mills et al. 1993). Brown trout were intentionally released into the Pere Marquette River, a tributary of Lake Michigan, in 1883 (Emery 1985) as a potential sportfish; in the same year the fish was released accidentally from a fish hatchery into the Genesee River, a tributary of Lake Ontario. Most species introductions, however, have been unintentional and are linked directly to the development of the global economy. Population growth spurred the need to transport goods to and from the Great Lakes basin and ultimately led to the opening of the St. Lawrence Seaway in 1959. The seaway provided a new pathway for the transport of goods from all parts of the world, but has inadvertently facilitated the introduction of many species that have altered the ecological nature of the Great Lakes.

GLOBALIZATION AND TRANSCOCEANIC SHIPPING

Transoceanic shipping has been the most important vector of introduction of NIS to the Great Lakes since the completion of the St. Lawrence Seaway, accounting for about 65 percent of all introductions since that time (data from Mills et al. 1993; Ricciardi 2001, 2006) (Fig. 6.2). The discovery of Eurasian ruffe (*Gymnocephalus cernuus*) and zebra mussel (*Dreissena polymorpha*) in the late 1980s prompted the Great Lakes

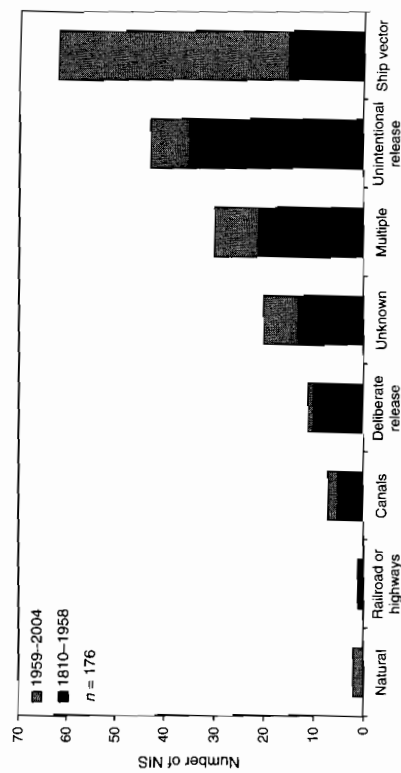


Figure 6.2 Vectors of introduction of non-indigenous species (NIS) to the Great Lakes prior to (black bars) and since (gray bars) the opening of the St. Lawrence Seaway in 1959.

Fishery Commission and the International Joint Commission to respond by calling the governments of the United States and Canada to develop a policy to reduce introductions of NIS from ballast water (Reeves 1999). Voluntary ballast water exchange guidelines were issued by Canada in 1989, and mandatory regulations were issued by the United States in 1993 (U.S. Coast Guard 1993). The legislation, specific to vessels entering the Great Lakes, mandated that vessels arriving from outside the exclusive economic zone (200 nautical miles [370 km] from shore) with declarable ballast water on board (BOB) must conduct open-ocean ballast exchanges if the water was to be subsequently discharged within the Great Lakes system; post-exchange ballast water must possess a salinity of no less than 30 parts per thousand (Locke et al. 1991, 1993; U.S. Coast Guard 1993). The premise behind ballast water exchange was that most freshwater organisms resident in ballast tanks would be purged and remaining organisms would be killed by osmotic stress when saltwater was loaded into the tanks. Ongoing tests to assess the efficacy of ballast water exchange for BOB vessels exchanging freshwater for saline water indicated that the process is likely highly effective and should dramatically reduce risk of invasion of the Great Lakes via this mechanism (Gray et al. 2006).

Contrary to expectations, the discovery rate of ship-vectored NIS increased following implementation of the ballast exchange policy (Holeck et al. 2004). The reasons for this increase are not clearly understood, but one possible explanation is that more than 90 percent of vessels that entered the Great Lakes during the 1990s declared "no

ballast on board" (NOBOB) and were not required to exchange ballast, although their tanks contained residual sediments and water that would be discharged in the Great Lakes (Colautti et al. 2003). NOBOB vessels carry cargo, reflecting the transport and globalization of goods, but can carry up to 60 tonnes of sediment and water that may harbor organisms and viable resting stages (Bailey et al. 2003, 2004, 2005). Recent studies demonstrate that NOBOB ships carry diverse assemblages of non-indigenous invertebrates (as free-swimming adults and resting eggs) at low densities in residual water and residual sediments (Bailey et al. 2003, 2004, 2005). It is still not clear whether these sources are large enough to seed new populations in the Great Lakes.

Though the historical trend in reported discovery of new NIS in the Great Lakes has been linear (Fig. 6.3A), the number of NIS introduced via the ship vector has accelerated since the opening of the St. Lawrence Seaway (Fig. 6.3B). It remains unclear whether this pattern reflects actual establishment rates of NIS in the lakes, or is an artifact. Two issues that may cloud the establishment rate are research intensity and time lags. Increased research intensity could partially account for the elevated rate of discovery during the 1990s because the issue of NIS introductions has received considerably more attention in both the scientific sector and popular press in recent decades. However, some of the species (e.g., *Cercopagis pengoi*) discovered in this recent period include taxa that are easily found and identified, thus it is unlikely that they existed in the lakes for years prior to discovery. Similarly, time lags could have an influence on discovery rates if the interval between establishment and discovery has changed through time. This interval may have been reduced in recent years owing to increased scientific investigation of NIS in the lakes. Alternatively, invasion rate might increase if positive interactions involving established NIS or native species facilitated entry of new NIS. Ricciardi (2001) suggested that such a scenario of "invasional meltdown" is occurring in the Great Lakes, although Simberloff (2006) cautioned that most of these cases have not been proven. Of all the Great Lakes (including Lake St. Clair), Lake Superior receives a disproportionate number of discharges by both BOB and NOBOB ships (70 percent), yet it has sustained surprisingly few initial invasions (Colautti et al. 2003). This lake may pose a formidable environment for potential invaders and thus remains poorly invaded despite intense propagule pressure exerted upon it. Conversely, the waters connecting Lakes Huron and Erie are an invasion "hotspot" despite receiving disproportionately few ballast discharges (Grigorovich et al. 2003). If invasional meltdown is occurring

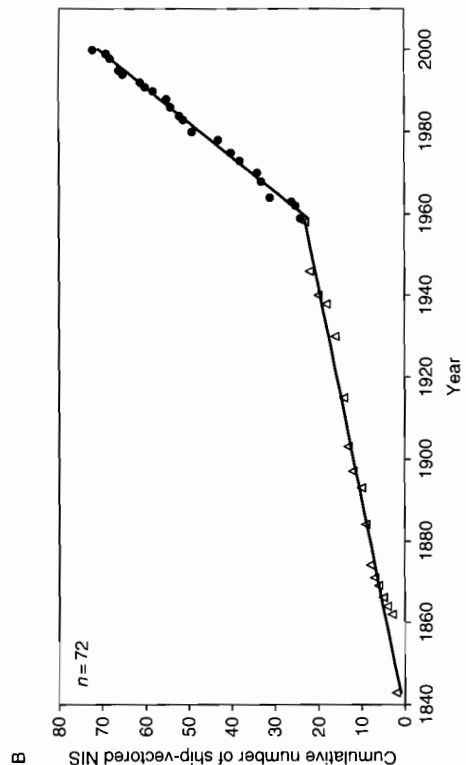
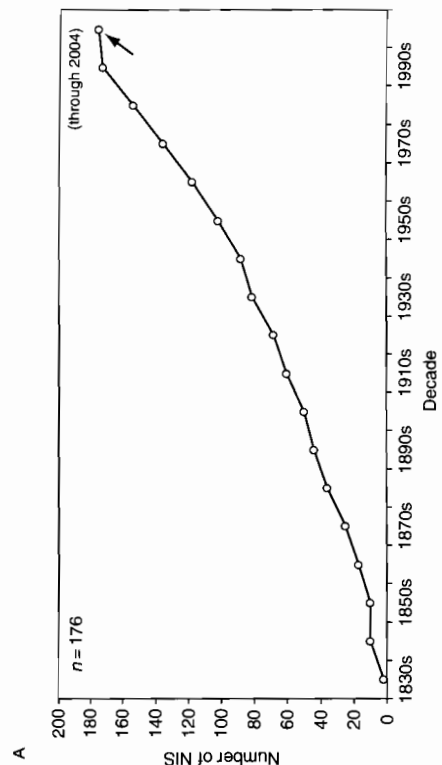


Figure 6.3 Accumulation of NIS in the Great Lakes since 1843 introduced by all vectors (A) and the ship vector only (B). The rate of ship-vectored introductions from 1959 to 2000 is more than five times the rate during the period 1843–1958.

it appears to be limited to the lower lakes. It should be noted, however, that many other hypotheses can account for the same pattern as that developed by invasional meltdown.

The transport of Ponto-Caspian species via the ship vector is consistent with patterns of transoceanic shipping. Between 1986 and 1998, most transoceanic vessels entering the Great Lakes arrived from European ports in the lower River Rhine region, on the North Sea and on the Baltic Sea (Colautti et al. 2003). However, most NIS discovered in

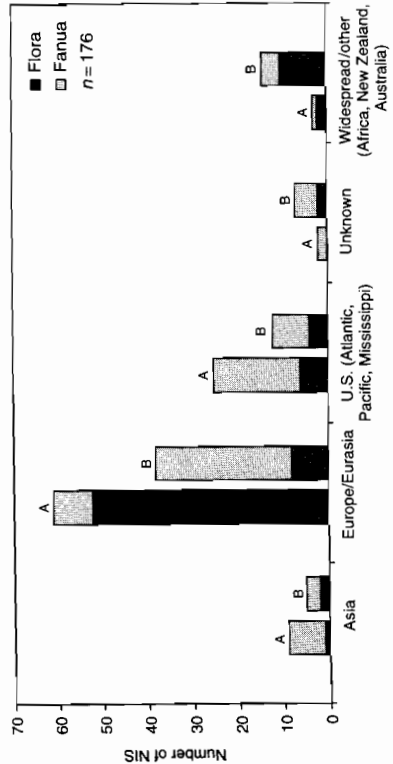


Figure 6.4 Donor regions for floral (black bars) and faunal (gray) NIS introduced to the Great Lakes from 1810 to 1958 (A) and 1959 to 2004 (B). The St. Lawrence Seaway opened in 1959.

the Great Lakes during that time were native to the Ponto-Caspian region (Ricciardi and MacIsaac 2000; MacIsaac et al. 2001; Ricciardi 2006) (Fig. 6.4). Ongoing invasion of key port areas on the North Sea by (e.g., Rotterdam, Antwerp) and the southern coast of the Baltic Sea by species native to the Ponto-Caspian region provide opportunities for these taxa to invade the Great Lakes in secondary invasions (Cristescu et al. 2001, 2004; Bij de Vaate et al. 2002; Leppäkoski et al. 2002). Although the last port of call for NOBOB vessels was more likely a ballast water recipient than a ballast water donor, ships operating in the Rhine–North Sea–Baltic Sea region visit several ports there, and this could explain why NOBOB ships arriving from those regions could still represent a strong vector for the entry of Ponto-Caspian NIS to the Great Lakes, as freshwater residuals and accumulated sediment in these vessels represent a mixture from ports recently visited. It should be noted that only a fraction of NOBOBs entering the Great Lakes do so with freshwater residuals, but this sub-vector appears to pose greater risk than that associated with invertebrates living in ballast sediments or which are present as viable, diapausing eggs (Duggan et al. 2005).

INVASION HISTORIES OF PONTO-CASPIAN SPECIES IN NORTH AMERICA AND EURASIA

The dispersal of Ponto-Caspian species to Eurasian and European inland waters has spanned the course of several thousand years, while the invasion of North American waters began only decades ago.

Dispersal rates differ greatly because of differences in the type and degree of human facilitation; despite this fact, patterns of geographic dispersal of Ponto-Caspian invaders in the Great Lakes show similarities to those observed in Europe and Eurasia. Zebra mussel, *Echinogammarus*, round goby, and *Cercopagis* have all exhibited wide-spread and rapid expansion of their geographic ranges since their introduction to North American waters. Conversely, quagga mussel (*Dreissena rostriformis*) dispersal has been limited. Where quagga mussels have invaded areas occupied by zebra mussels, the former has generally become the dominant dreissenid (Mills et al. 1996, 2003). Ricciardi and Rasmussen (1998) argued that invasion history can be used as a predictive criterion for determining whether a species can invade a target region. We suggest that the pattern of dispersal of a species will also be similar in both donor and recipient regions regardless of geography if these organisms utilize human-mediated dispersal mechanisms. Indeed, at the same time that the quagga mussel dispersed in North America, it began to spread by ship-mediated vectors up and down the Volga River in Russia (Orlova et al. 2005).

Zebra and quagga mussels

By the early Holocene, the range distribution of the zebra mussel encompassed a small portion of its contemporary distribution in the Black, Azov, and Caspian drainage basins (Starobogatov and Andreeva 1994). The zebra mussel expanded its range during the Holocene in association with human activities. Ancient boat traffic on the Danube, Dnieper, Don, and Volga Rivers likely facilitated its dispersal into these drainages. In 1769, Pallas first described populations of this species from the Caspian Sea and the Ural River. By the late eighteenth century and early nineteenth century, zebra mussel had spread to most major drainages of Europe using the vast network of canals. Zebra mussels appeared in Great Britain in 1824, and then in Leiden (1826), the lower Doru River in Portugal (1829), and many locations throughout the Netherlands and Belgium, France (Nor), Denmark (Copenhagen), Sweden, Finland, Italy, and the rest of Europe (Strayer 1991; Starobogatov and Andreeva 1994). Despite its extensive range throughout Europe and Eurasia (Fig. 6.5A), expansion of *D. polymorpha* northward has been limited by low water temperatures beyond latitudes 58° N (Starobogatov and Andreeva 1994), although Orlova and Panov (2004) reported its establishment in the Neva Estuary in the eastern Gulf of Finland.

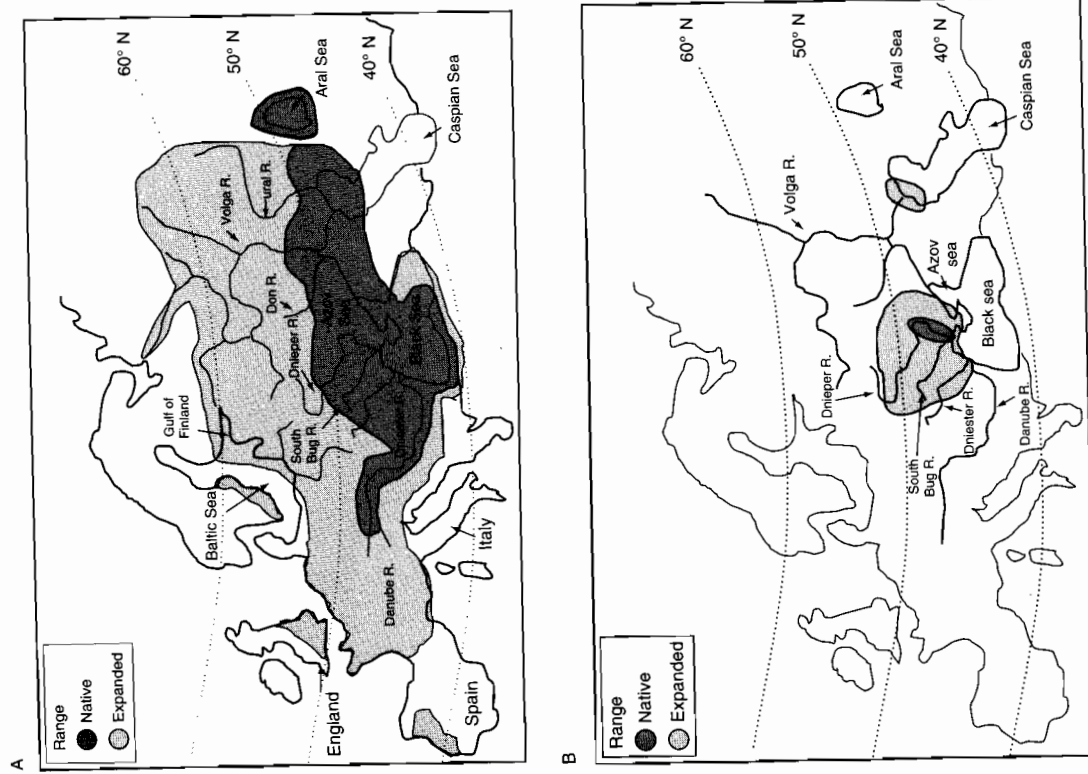


Figure 6.5 Generalized distribution of zebra mussel (A, C) and quagga mussel (B, D) in Eurasia (A, B) and the Great Lakes (C, D).

The quagga mussel, *Dreissena rostriformis bugensis*, was discovered in the Bug portion of the Dnieper-Bug estuary near Nikolaev in the Ukraine by Andrusov (1890). According to Zhuravel (1967), this mussel was first introduced into the Dnieper River attached to ship hulls in 1941. Since the 1940s, the quagga mussel has spread from the South

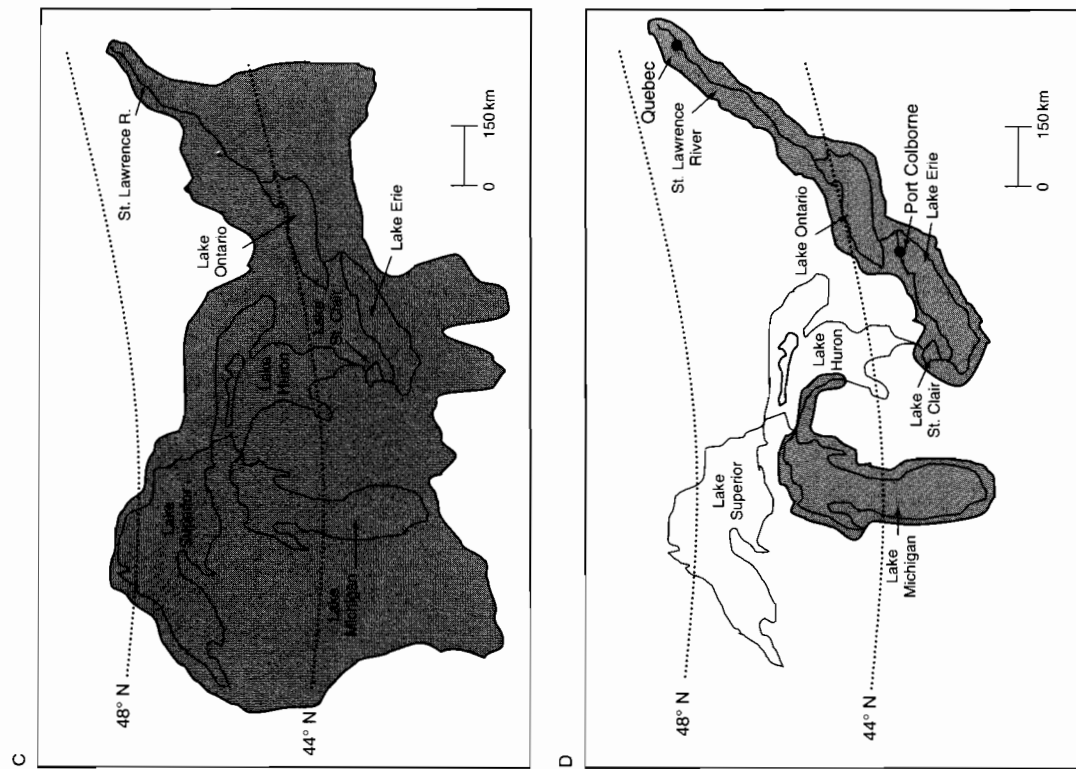


Figure 6.5 (Cont.)

Bug River and the lower Ingulets River into the Dnieper River drainage to regions that earlier had only *D. polymorpha* (Mills et al. 1996). It subsequently expanded its range elsewhere north of the Black Sea and into the northern Caspian Sea and Volga River Delta (1994–97) as well as to the middle (Samara region, 1992) and upper Volga River drainage (Orlova et al. 2005). To date, the geographic distribution of the quagga mussel in Eurasia has been limited to the Ponto-Caspian

region, and its range expansion has been relatively slow. Despite its limited geographic distribution (Fig. 6.5B), the quagga mussel can dominate habitats that were once dominated by zebra mussels (Mills et al. 1996; but see Zhulidov et al. 2006).

Zebra mussels, first collected from the Canadian waters of Lake St. Clair in 1988 (Hebert et al. 1989) (Fig. 6.5C), had been found in each of the Great Lakes by 1990. After 1992, populations of zebra mussels rapidly spread throughout the eastern United States. In contrast, the quagga mussel, first collected at Port Colborne in Lake Erie in 1989 (Mills et al. 1999), had expanded its range only from Lake St. Clair eastward to Quebec City on the St. Lawrence River (Fig. 6.5D) in the 4 years after its discovery. However, habitats once dominated by zebra mussels are now dominated by quagga mussels, a trend that parallels that in the Dnieper River basin in Ukraine (Mills et al. 1996, 1999, 2003).

Round goby

Round gobies (*Apolonia* (*Neogobius*) *melanostomus*) are endemic to the Ponto-Caspian region, occurring in the open parts of the Caspian Sea, along the Black Sea and Azov Sea shelf, and in their lagoons and river estuaries (Miller 1986) (Fig. 6.6A). They were first found in the Baltic Sea (Puck Bay, Gulf of Gdansk) in 1990 (Skora and Stolarksi 1993). In the Great Lakes, round gobies were first collected in the St. Clair River on the Michigan–Ontario border in 1990 (Jude et al. 1992) (Fig. 6.6B). By 1994, the round goby had spread into northern Lake St. Clair and was abundant in the St. Clair River. By 1997, they had spread to all the Great Lakes, three inland rivers in Michigan (Flint, Shiawassee, and Saginaw), and the Chicago Sanitary and Shipping Canal (Steingraeber et al. 1996). In 1998, round gobies were reported from numerous sites along the east shore of Michigan in Lake Huron and in Michigan's Upper Peninsula at Port Inland and in Little Bay de Noc. In 1994, they appeared in southern Lake Michigan in the Calumet–Chicago area of Illinois, and in 1999 near the confluence of the Calumet Sag Channel and the Chicago Sanitary and Shipping Canal. In Indiana, round gobies were found in the Grand Calumet River in 1993. Trawls fished 200 individuals in October 1994 at Fairport, Ohio, in Lake Erie, and by 1995, more than 3000 individuals were collected, indicating that the population had expanded greatly. Round gobies expanded eastward to just west of Erie, Pennsylvania, in 1996, in the eastern basin of Lake Erie at Buffalo, New York, by 1998, and they now have been identified at numerous sites along the north shore of Lake Erie. Round gobies

from the Wisconsin waters of St. Louis Bay, Lake Superior. Adult specimens were also found in Duluth Harbor, Minnesota, from 1996 to 1999.

Cercopagis pengoi

Cercopagis pengoi, commonly known as the fishhook flea (MacIsaac *et al.* 1999), is endemic to fresh and brackish waters of the Black, Azov, Caspian, and Aral Sea basins, and to coastal lakes and reservoirs on the Don and Dnieper Rivers (see Mordukhai-Boltovskoi and Rivier 1987) (Fig. 6.7A). Damming, construction of reservoirs and canals, shipping, and the intentional stocking of invertebrates in the Dnieper, Don, and Many Rivers have facilitated dispersal of this organism in eastern Europe (Grigorovich *et al.* 2000). *Cercopagis pengoi* has established permanent populations in the fresh waters of the Kakhovka, Zaporozhsk, Kremenshug, Tsimlyansk, and Veselovsk reservoirs on the Don and Dnieper rivers (Krylov *et al.* 1999; Grigorovich *et al.* 2000). This onychopod has invaded the lower reaches of the Danube, Dniester, southern Bug, Dnieper, and Volga Rivers as well as coastal lakes fringing the Black Sea (Mordukhai-Boltovskoi 1968; Mordukhai-Boltovskoi and Rivier 1987; Rivier 1998). In 1992, *C. pengoi* was reported in the Baltic Sea (Parnu Bay and the Gulf of Riga) (Ojaveer and Lumberg 1995). Its range has continued to expand in Europe, as evidenced by its presence in coastal areas off Kotka in the Gulf of Finland (Uitto *et al.* 1999), the Neva Estuary and the open sea area in the eastern Gulf of Finland (1995 and 1996) (Avinski 1997), and the Baltic Sea proper (1997) (Gorokhova 1998; MacIsaac *et al.* 1999).

Cercopagis pengoi was first detected in the Great Lakes in Lake Ontario in 1998 (MacIsaac *et al.* 1999). It was observed throughout the lake in 1998 and 1999, with density peaks occurring in August and September (Makarewicz *et al.* 2001). In 1999, it appeared in Lake Michigan in two areas: Waukegon Harbor (Illinois) and Grand Traverse Bay (Michigan) (Charlebois *et al.* 2001). It also spread into the Finger Lakes region of New York State (Makarewicz *et al.* 2001). *Cercopagis* was found in western Lake Erie in 2001 (Therriault *et al.* 2002) and central Lake Erie (Fairport, Ohio, and Erie, Pennsylvania) in 2002 (Fig. 6.7B).

Echinogammarus ischnus

The euryhaline gammarid amphipod *Echinogammarus ischnus* is native to the Caspian Sea, fresh and estuarine regions of the Black and Azov Seas,

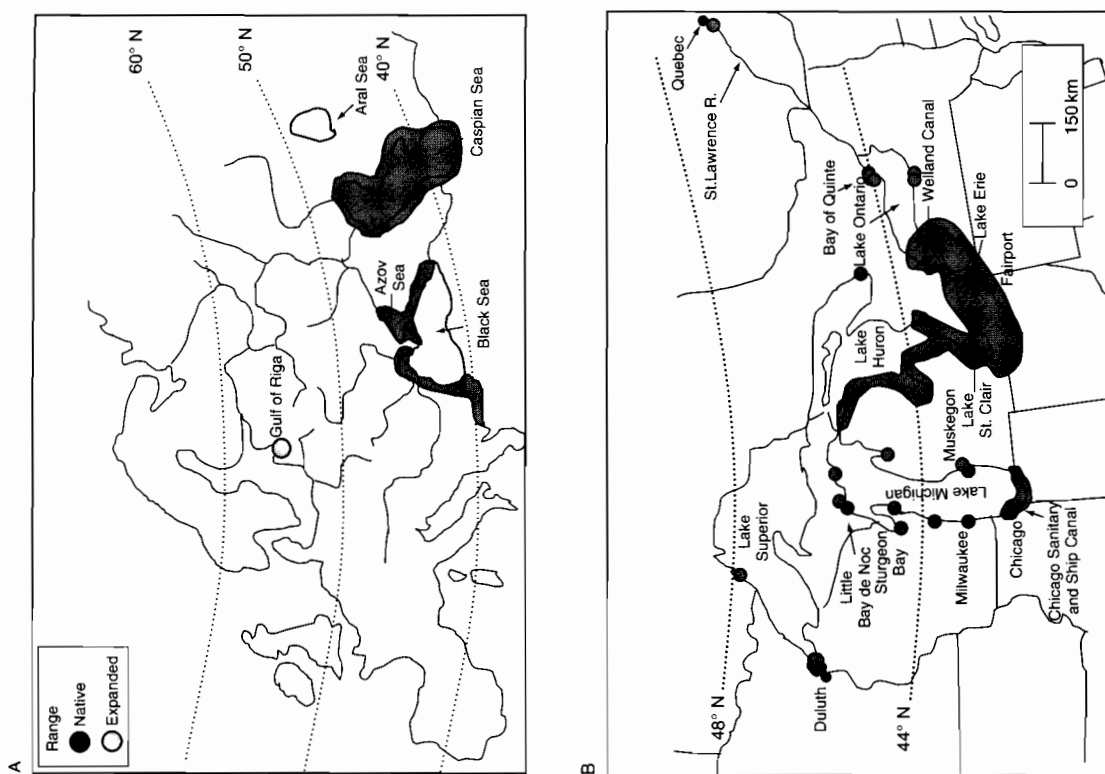


Figure 6.6 Generalized distribution of the round goby in Eurasia (A) and the Great Lakes (B).

have continued to expand their eastward distribution with sightings in the Welland Canal (1998), the St. Lawrence River near Quebec (1997), and northeastern Lake Ontario in the Bay of Quinte (1999). Discontinuity in the geographic spread of the round goby became evident in July 1995 when a single individual was collected in trawls

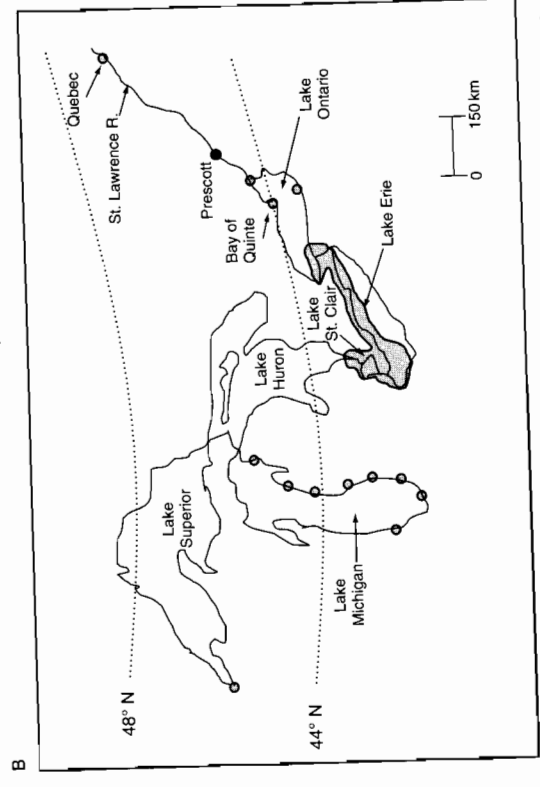
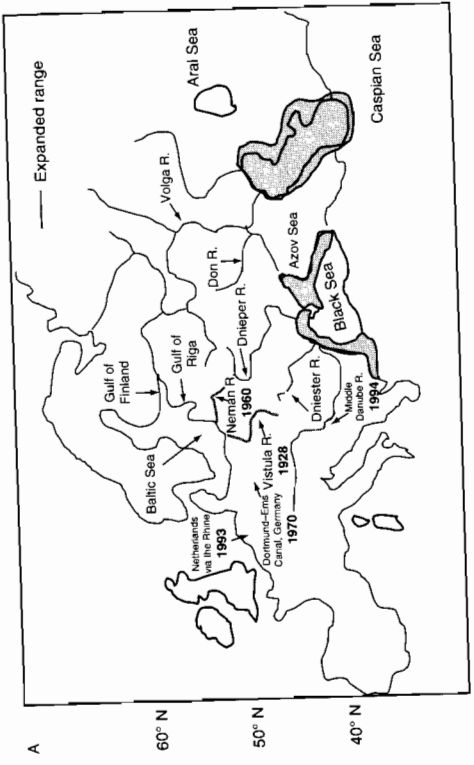


Figure 6.8 Generalized distribution of *Echinogammarus ischnus* in Eurasia (A) (for image in colour please see plate section) and the Great Lakes (B).

below Warsaw (Jarocki and Demianowicz 1931). Over 30 years later (1960) *Echinogammarus* had colonized the lower Neman River via the Neman-Pripet Canal. In the 1970s, this amphipod was discovered in the Dortmund-Ems Canal in Germany. By the late 1970s, it had established populations in the Dnieper, Dniester, Southern Bug, Danube, Don, and Volga Rivers (Mordukhai-Boltovskoi 1960, 1979a). *Echinogammarus* has also been widely introduced (deliberately and

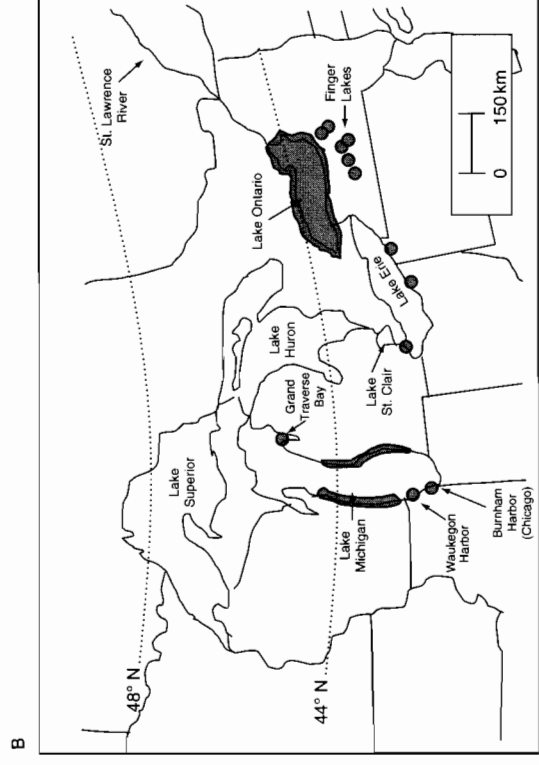
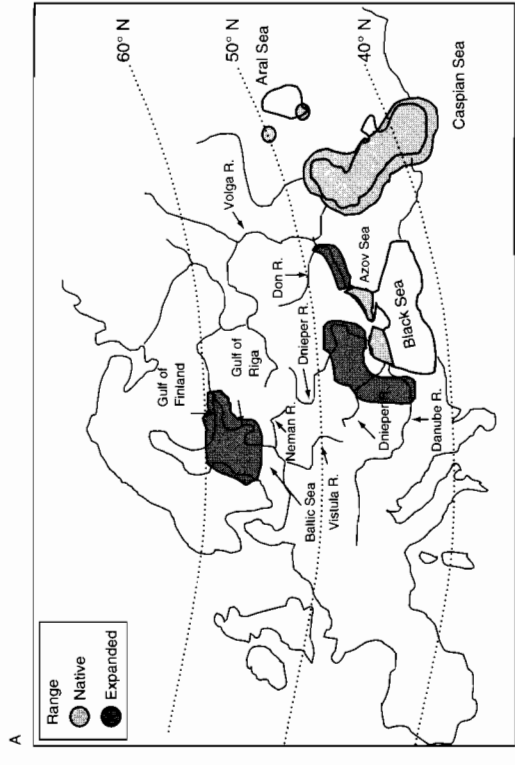


Figure 6.7 Generalized distribution of *Cercopagis pengoi* in Eurasia (A) and the Great Lakes (B).

areas north of the Black Sea (Jazdzewski 1980), and both Russia and the Ukraine (Konopacka and Jesionowska 1995) (Fig. 6.8A). Relict populations occur in some Romanian and Bulgarian lakes. *Echinogammarus* was first observed outside its native range in 1928, when it entered the Pripet-Bug canal system and was discovered in the Vistula River

...plants
(musko 1994) and recently migrated to the Netherlands from Germany via the River Rhine (Van den Brink *et al.* 1993).

The first published report of *Echinogammarus ischnus* in North America was from the Detroit River in 1995 (Witt *et al.* 1997) (Fig. 6.8B). However, analysis of archived samples revealed the presence of the species from western Lake Erie in 1994 and possibly as early as 1993 (van Overdijk *et al.* 2003). Dermott *et al.* (1998) reported this species to be "widespread" from the south end of Lake Huron to Lake Erie and Lake Ontario and the St. Lawrence River at Prescott. *Echinogammarus* was collected from several locations in Lake Michigan, during 1998-99, and established populations were reported in Lake Huron, Lake Ontario, and the upper St. Lawrence River in 2000 (USGS 2005). This amphipod is now common in nearshore areas of the western two-thirds of Lake Ontario, and its eastern range extends to Quebec City on the St. Lawrence River (Vanderploeg *et al.* 2002).

IMPACTS OF PONTO-CASPIAN SPECIES ON GREAT LAKES FISHERIES

The invasion of the Great Lakes by Ponto-Caspian species has altered ecosystem structure and function in several ways. First, colonization by zebra and quagga mussels has increased structural complexity and deposition of organic matter, benefiting benthic invertebrates in eastern Lake Erie, Lake St. Clair, Lake Ontario, and Lake Michigan (Griffiths *et al.* 1991; Stewart and Haynes 1994; Dermott and Kerec 1997; Kuhns and Berg 1999; Bially and MacIsaac 2000). Also, filtering activity by *Dreissena* spp. has increased water clarity, leading to increased vectoring of lower trophic level production to benthic habitats (Nalepa *et al.* 2000). With increased light penetration, dreissenids have indirectly increased benthic algal production (Fahnenstiel *et al.* 1995a; Lowe and Pillsbury 1995), enhanced benthic-pelagic coupling (MacIsaac *et al.* 1999), and increased macrophyte growth (Skubinna *et al.* 1995). In Saginaw Bay, Lake Huron, a reduction in primary production by phytoplankton was nearly compensated by increased benthic algal production (Fahnenstiel *et al.* 1995a, b). Finally, dreissenid mussel establishment may facilitate the success of coevolved Ponto-Caspian invaders (round goby and *Echinogammarus ischnus*) (Ricciardi 2001) by providing food and habitat, respectively. Round gobies prey on native

the potential to negatively affect restoration of lake trout populations (*namaycush*) (Chotkowski and Marsden 1999) and lake sturgeon (*Acipenser fulvescens*) (Nichols *et al.* 2003). *Echinogammarus* has replaced the native amphipod *Gammarus fasciatus* in the St. Clair, Detroit, and Niagara Rivers and in Lake Ontario at the mouth of the Welland Canal (Dermott *et al.* 1998), the effects of which are currently not clear. *Cercopagis pengoi* predation on zooplankton has been documented in the Gulf of Riga, where Leppäkoski *et al.* (2002) correlated its arrival with a decline in *Bosmina coregoni maritima*. Similar declines of small zooplankton, mainly juvenile cyclopoid and calanoid copepods and *Bosmina*, have been reported in Lake Ontario in association with elevated densities of *C. pengoi* (Benoît *et al.* 2002; Laxson *et al.* 2003). Fish in both systems feed on *Cercopagis*, although young-of-the-year alewife (less than 66 mm total length) in the Great Lakes have difficulty feeding on *C. pengoi* because of its long caudal spine (Bushnoe *et al.* 2003). Thus *Cercopagis* may depress zooplankton prey, resulting in decreased alewife growth and lower overwinter survival (O'Gorman *et al.* 1997).

Increased water clarity, resulting first from phosphorus abatement and enhanced later by dreissenid mussel grazing/filtering, represents one of the most dramatic ecological changes in the recent history of the Great Lakes. Great Lakes fishes are now exposed to much higher light levels than existed prior to dreissenid mussel establishment, and this can have profound effects on predator-prey interactions. For example, the opossum shrimp (*Mysis relicta*) exhibits remarkable diel migration behavior, moving from deep water to feed on epilimnetic and metalimnetic zooplankton during the night (Beeton and Bowers 1982). With increased light penetration, *Mysis* could remain deeper in the water column because of their high sensitivity to light (Gal *et al.* 1999), thus affecting their availability to prey on fish. Increases in water clarity have also altered fish distribution, with species such as alewife and rainbow smelt shifting to deeper waters in the springtime (O'Gorman *et al.* 2000). We can only speculate that large-scale changes in light conditions have had significant impact on Great Lakes fish communities by altering prey and predator spatial and temporal distributions and predator-prey interactions.

Ecological surprises can occur in ecosystems from both compounded effects of multiple perturbations (e.g., climate warming and invasion by NIS: Paine *et al.* 1998) and interactions between established invaders (Ricciardi 2001). For example, dreissenid mussels and round goby may be linked to recent outbreaks of Type E botulism in lakes Erie

... which have resulted in both fish kills and the deaths of tens of thousands of waterfowl (primarily loons, mergansers, and gulls). The diets of some birds have become increasingly dominated by round gobies, which likely transfer the botulin toxin - produced by the bacterium *Clostridium botulinum* - from the quagga mussels upon which they feed. Scavenging gulls are affected through their consumption of dead fish that have already succumbed to the toxin themselves, either directly through the ingestion of dreissenid mussels or indirectly through the ingestion of other mussel-eating fish. Dreissenid mussels not only concentrate the toxin as they filter water proximal to the sediments that contain the *Clostridium* bacterium, but they may also contribute to anoxic conditions that favor the proliferation of the bacterium by generating large amounts of fecal deposits.¹ Finally, the success of round goby and *Echinogammarus* was likely enhanced by the presence of dreissenid mussels (Ricciardi and MacIsaac 2000). The result is an accelerated rate of invasion, or invasional meltdown (Ricciardi 2001), enhanced by facilitative interactions between coevolved NIS, that leads to future uncertainty about how large-scale ecosystems such as the Great Lakes will respond.

CONCLUSIONS AND FUTURE CHALLENGES

The effects of globalization have taken the Great Lakes on an unpredictable ecological path, particularly through the introduction of NIS. Since the early nineteenth century, over 176 NIS have established, and the apparent invasion rate has increased in association with an expanding range of anthropogenic activity. Global trade (i.e., international shipping) has been identified as the primary mechanism for the introduction of NIS over the past four decades. The prevalence of Ponto-Caspian introductions in the past two decades, combined with the fact that most ships arrive from European ports, indicates that secondary transfer routes (where Ponto-Caspian species establish first in ports on the Baltic Sea before being transported to North America) are an important factor.

The biological stressors associated with globalization, including the invasion by dreissenid mussels and other exotic species, have caused profound ecological changes in Great Lakes ecosystems. Responses to these stressors have led to significant changes in Great

Lakes fish communities. For example, dramatic springtime shifts in alewife and rainbow smelt distribution have occurred in response to changes in water clarity, stocks of native lake whitefish populations have dwindled, and the partitioning of energy to fish in the face of newly established exotics has become more complex, especially in Great Lakes' nearshore habitats. Globalization and biological invasions will continue to affect Great Lakes fisheries in the future. At present, the food webs of the Great Lakes are composed of native species and naturalized NIS that share no evolutionary history. With so many Great Lakes fish communities and supporting food web organisms considered non-native, historical food webs are no longer useful for understanding species interrelationships and future outcomes of biological stressors. Consequently, as long as globalization, biological invasions and large-scale ecological changes continue to dominate Great Lakes ecosystems, the need for scientific understanding and the desire to manage fisheries in these large water bodies in the coming decades will be enormous. To this end, the challenge in an era of globalization is clear: scientists and managers must engage in the development of new ecological paradigms and seek new insights into our understanding of functionality if there is any hope of meeting the need to manage fish and other elements of Great Lakes ecosystems in the future.

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¹ Helen Domske, New York Sea Grant, Buffalo, New York, personal communication.

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