Bridging Troubled Waters: Biological Invasions, Transoceanic Shipping, and the Laurentian Great Lakes

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Release of contaminated ballast water by transoceanic ships has been implicated in more than 70% of faunal nonindigenous species (NIS) introductions to the Great Lakes since the opening of the St. Lawrence Seaway in 1959. Contrary to expectation, the apparent invasion rate increased after the initiation of voluntary guidelines in 1989 and mandatory regulations in 1993 for open-ocean ballast water exchange by ships declaring ballast on board (BOB). However, more than 90% of vessels that entered 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. Lake Superior receives a disproportionate number of discharges by both BOB and NOBOB ships, yet it has sustained surprisingly few initial invasions. Conversely, the waters connecting Lakes Huron and Erie are an invasion hotspot despite receiving disproportionately few ballast discharges. Other vectors, including canals and accidental release, have contributed NIS to the Great Lakes and may increase in relative importance in the future. Based on our knowledge of NIS previously established in the basin, we have developed a vector assignment protocol to systematically ascertain vectors by which invaders enter the Great Lakes.

Keywords: Great Lakes, ship vector, ballast, nonindigenous species, vector assignment protocol

Biological invasions by nonindigenous species (NIS), a global environmental problem, have damaged both aquatic and terrestrial ecosystems (Mills et al. 1994, Kitchell et al. 1997, D'Antonio and Kark 2002). Negative ecological impacts on aquatic ecosystems, the focus of increasing study in recent decades, include dramatic modifications of food webs (Ricciardi 2001, Vanderploeg et al. 2002, Mills et al. 2003), alteration of biogeochemical cycles (Johengen et al. 1995, Arnott and Vanni 1996), and declines in native biodiversity (Kitchell et al. 1997, Ricciardi et al. 1998, Rahel 2002, Yan et al. 2002). Impacts to socioeconomic sectors can also be significant and include transmission of pathogenic NIS to humans and wildlife (McCarthy and Khambaty 1994, Dalmazzone 2000, Hall and Mills 2000, Pimentel et al. 2000, Ruiz et al. 2000).

Numerous factors can affect invasion success, including similarity of donor and recipient environments, propagule pressure, species-level traits (e.g., population growth rate), habitat disturbance, and facilitative interactions with other species in the community (Simberloff and Von Holle 1999, Richardson et al. 2000, Maron and Vilà 2001, Ricciardi 2001, Kolar and Lodge 2002, Bruno et al. 2003, Daehler 2003, Duncan et al. 2003, Colautti and MacIsaac 2004). Propagule pressure, a factor with predictive power across taxa, relates the number of released individuals and the frequency of release events to invasion success and to patterns of NIS establishment (Kolar and Lodge 2001, Duncan et al. 2003). In aquatic ecosystems, NIS are transported at local, regional, and global scales through vectors such as transoceanic shipping, intentional release, migration through canals, escape from aquaculture, baitfish escape or release, and natural means. Most modern invasions are associated with human activities, and vector strength is typically related to the scale of human involvement (Ricciardi 2001).

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Collectively, the Laurentian Great Lakes represent perhaps the best-studied freshwater ecosystem in the world, with a well-documented history of human-mediated invasions (Mills et al. 1993, Ricciardi 2001, Grigorovich et al. 2003a). As such, these waters provide insights relevant to other large aquatic ecosystems. Here we use a coarse measure of propagule pressure—the discharge of ballast water by transoceanic ships—to explore spatial and temporal patterns of invasion. We also develop a vector assignment protocol that links life-history attributes of NIS established in the Great Lakes with possible transport mechanisms, providing a basis for assessing which vectors may be exploited by future invaders.

The ship vector: A brief history

More than 170 NIS have become established in the Great Lakes, entering through vectors that include shipping, canals, unintentional release, and deliberate release (Mills et al. 1993, 1994, Ricciardi 2001, Grigorovich et al. 2003a, Nicholls and MacIsaac 2004). However, transoceanic shipping is the primary mechanism responsible for the introduction of NIS to the Great Lakes over the last four decades (Mills et al. 1993, Ricciardi 2001). Since completion of the St. Lawrence Seaway in 1959, at least 43 NIS of animals and protists have become established in the Great Lakes, of which 73% have been attributed to the discharge of ballast water by transoceanic ships (Grigorovich et al. 2003a). Ships lacking cargo on international voyages may carry between 25% and 35% of their deadweight tonnage in the form of ballast water (Schormann et al. 1990). Ballast water provides trim and stability, but it is often contaminated with a suite of species that are moved between coastal areas throughout the world (Carlton 1985, 1989, 1996, Locke et al. 1991, 1993, Leppäkoski et al. 2002). Residual sediments present in both ballasted and non-ballasted vessels may harbor species in viable resting stages (Hallegraeff and Bolch 1991, Hallegraeff 1998, Hamer et al. 2000, Bailey et al. 2003). Also, NIS attached to ships' hulls or other surfaces represent a possible transport mechanism to marine coastal waters (Apte et al. 2000). This mechanism has been considered unimportant in the Great Lakes, because any freshwater or brackish-water species that foul seagoing

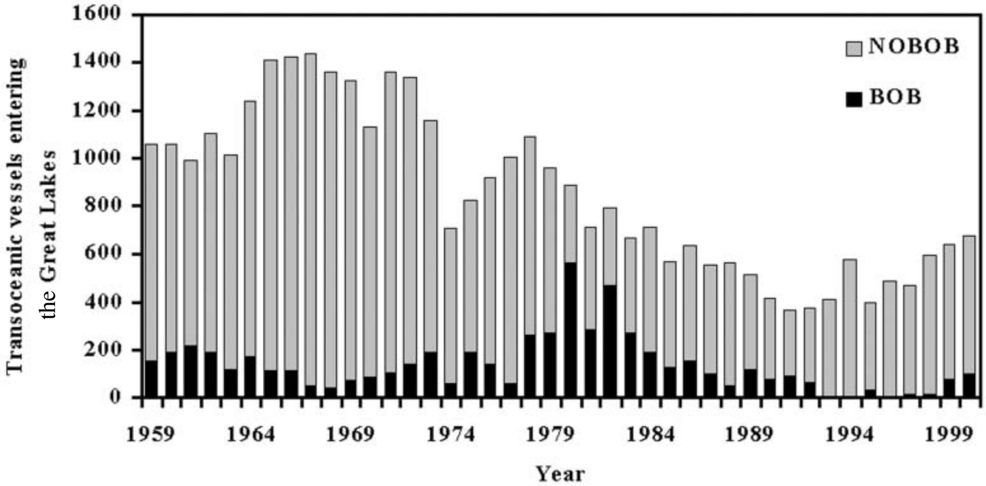

Figure 1. Vessel traffic into the Great Lakes between 1959 and 2000. The numbers of transoceanic vessels entering the system loaded with cargo and containing only residual water in ballast tanks (no ballast on board, or NOBOB) are shown in gray bars, while those entering the system loaded with ballast water and no cargo (ballast on board, or BOB) are shown in black bars. NOBOB ships constituted more than 90% of all traffic into the Great Lakes during the 1990s. From Grigorovich and colleagues (2003a).

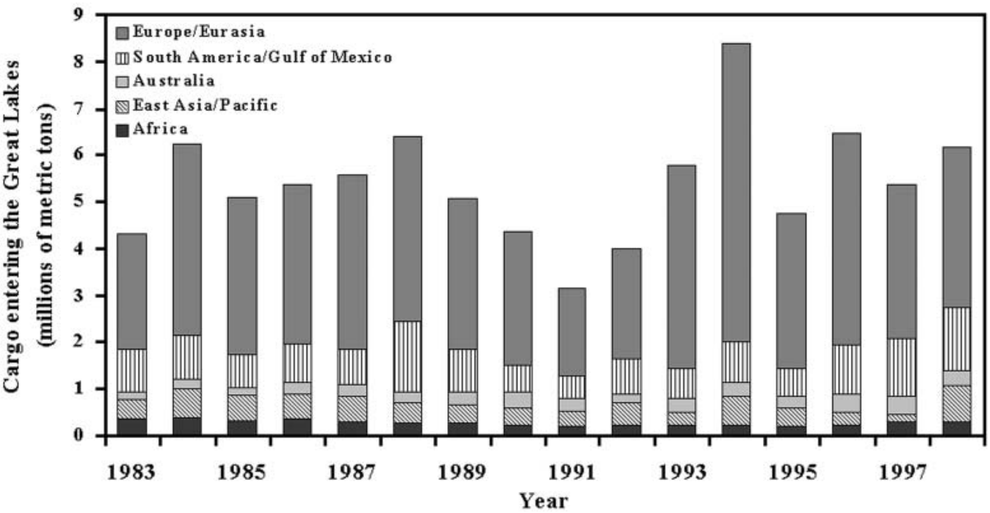

Figure 2. Amount of cargo entering the Great Lakes from Europe and Eurasia (dark gray), South America and the Gulf of Mexico (vertical stripe), Australia (light gray), East Asia and the Pacific (diagonal stripe), and Africa (black) between 1983 and 1998, in millions of metric tons. Vessels from Europe dominate inbound trade; most nonindigenous species identified in the Great Lakes during this period are of Eurasian origin.

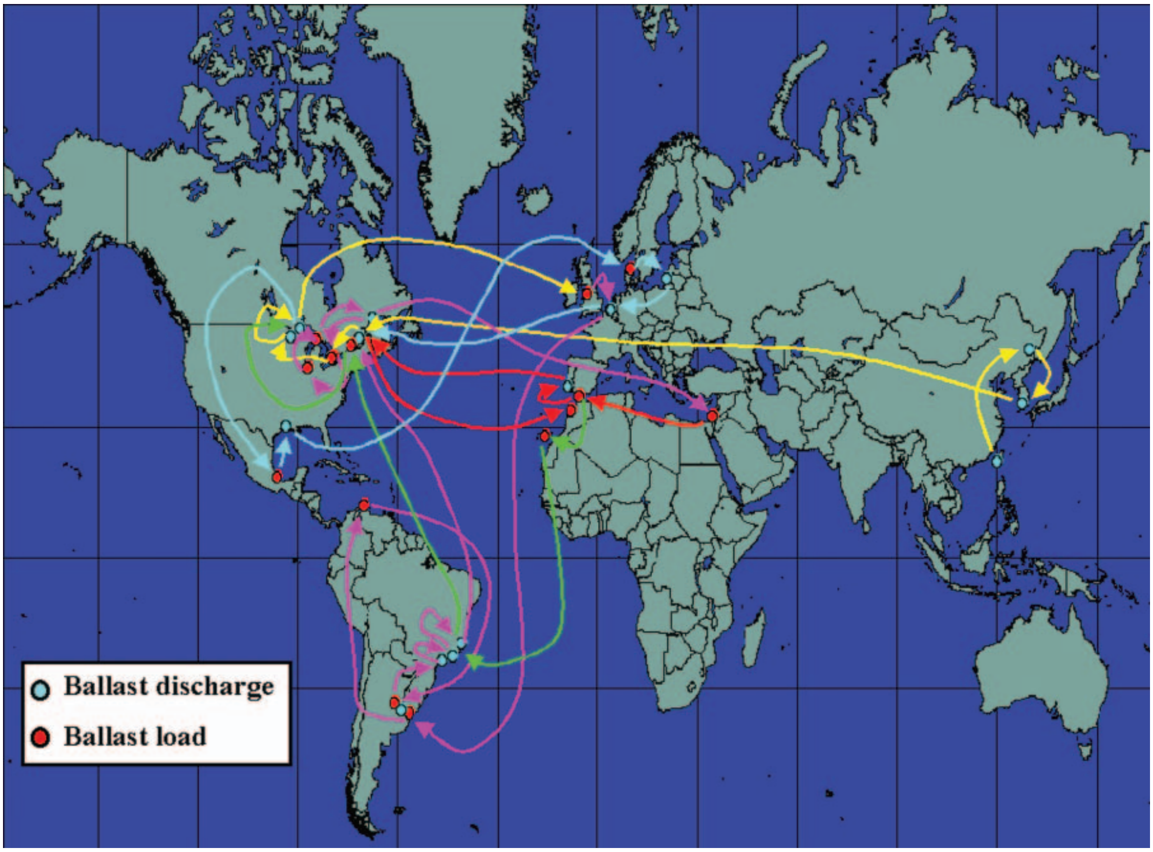

Figure 3. Global activity of a single transoceanic vessel over a 14-month period. Circles indicate sites where ballast water was loaded (red) or discharged (light blue).

ships would be expected to die during the extended exposure to highly saline water from the Atlantic Ocean, but this assumption remains poorly explored.

In 1988, in response to the discovery of Eurasian ruffe (*Gymnocephalus cernuus*) and zebra mussels (*Dreissena polymorpha*) in the Great Lakes, the Great Lakes Fishery Commission and the International Joint Commission called on the governments of the United States and Canada to reduce the introduction of NIS through ballast water (Reeves 1999). Canada issued voluntary ballast water guidelines in 1989, and the United States implemented mandatory regulations in 1993 (USCG 1993). Legislation specific to the Great Lakes effectively requires that oceangoing vessels with declarable ballast water (ballast on board, or BOB) conduct open-ocean ballast exchange if the water is to be subsequently discharged within the Great Lakes system; after the exchange, ballast water must possess a salinity of no less than 30 parts per thousand (Locke et al. 1991, 1993, USCG 1993). The premise behind ballast water exchange is that most freshwater organisms resident in ballast tanks are purged during the exchange, and the remaining organisms are killed by osmotic stress. Also, compared with coastal species, the substituted, open-ocean organisms are less likely to survive and reproduce in the Great Lakes. The Great Lakes legislation represents the most prescriptive ballast water law in the world and provides an opportunity to evaluate whether the Great Lakes have been sufficiently protected from new invasions as intended.

Donor regions and invasion hotspots

Throughout the 1990s, more than 90% of transoceanic vessels entering the Great Lakes carried cargo (Colautti et al. 2003). Although these ships are assumed to have no ballast on board (NOBOB), they retain on average 50 metric tons of residual sediment and 10 metric tons of residual water (Bailey et al. 2003). Only in 1980 and 1982 were there more BOB than NOBOB vessels (figure 1). The volume of transoceanic vessel traffic peaked at 1432 vessels in 1967 and declined to 675 vessels in 2000. Vessels entering the Great Lakes system arrived from approximately 460 different ports and five general regions: (1) Europe and Eurasia, (2) South America and the Gulf of Mexico, (3) Australia, (4) East Asia and the Pacific, and (5) Africa. Between 1983 and 1998, the bulk of inbound NOBOB ship traffic originated in Europe and Eurasia, followed by South America and the Gulf of Mexico (figure 2). Before the guidelines for ballast water exchange were enacted in 1989, ballasted vessels entering the Great Lakes contained water from their last one or two ports of call. However, penultimate port-of-call data for NOBOB vessels may not fully reflect invasion risk from a single donor region, as residual water and accumulated sediment in these vessels represent a

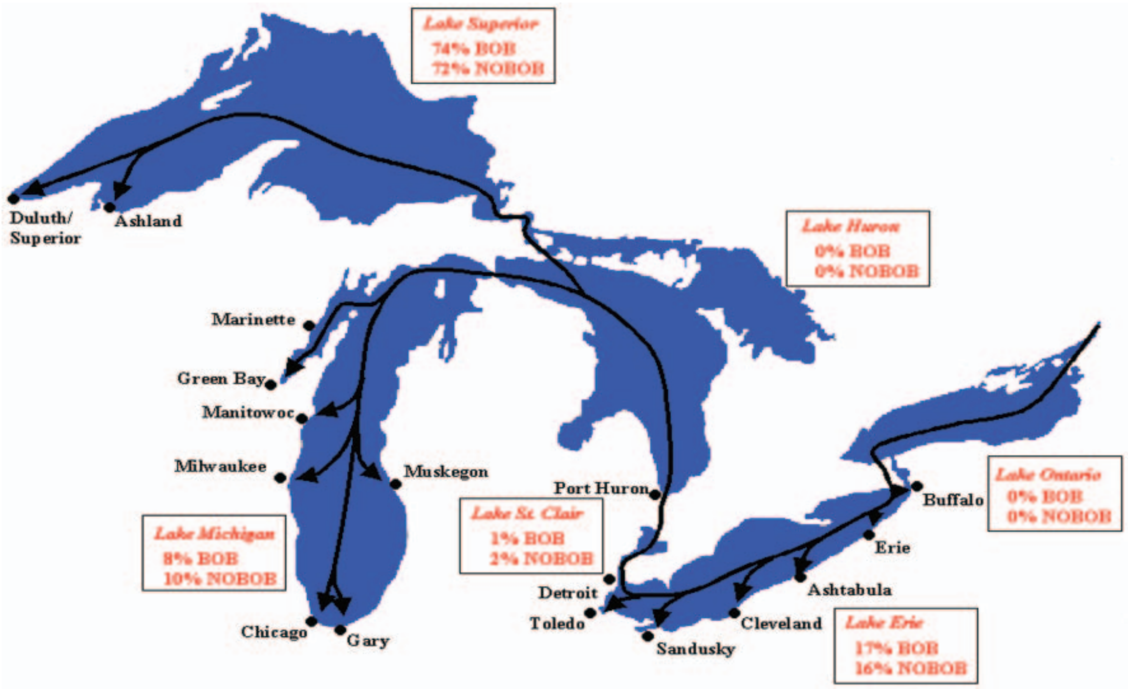

Figure 4. Traffic flow patterns and percentage of total ballast water discharges to US ports on the Great Lakes, 1981–2000, by transoceanic vessels either loaded with cargo and containing only residual water in ballast tanks (no ballast on board, or NOBOB) or without cargo and containing a full load of ballast water (ballast on board, or BOB). NOBOB ships usually stop at a series of ports while inbound, discharging cargo at each site and loading ballast water from the Great Lakes. This water mixes with residual water and sediment in ballast tanks and is later discharged at the terminal port where outbound cargo is loaded. Conversely, BOB ships proceed directly to their destination port, where the water is discharged as cargo is loaded for the outbound trip.

mixture from ports recently visited by a fleet that ranges globally (figure 3).

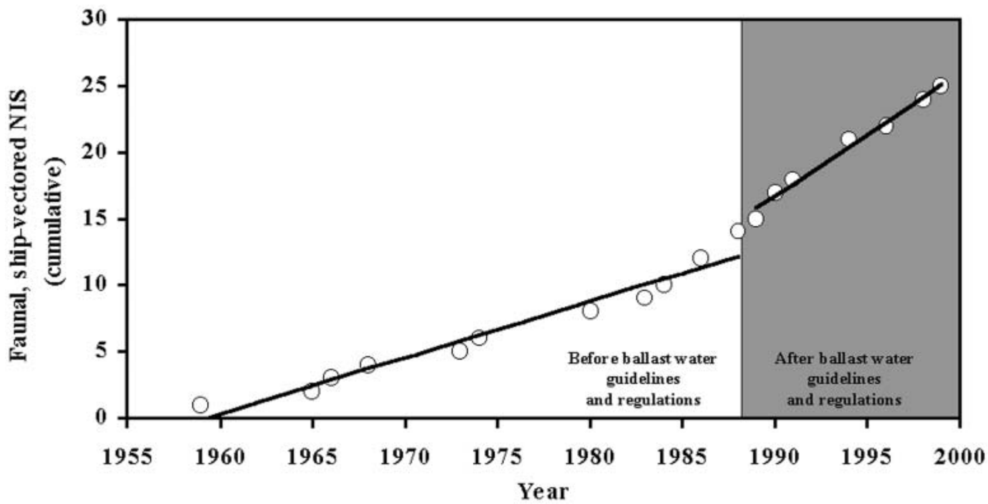

Figure 5. Accumulation of faunal nonindigenous species (NIS) introduced by ships to the Great Lakes between 1959 and 2000. Parasites that were introduced with their host species are not included. The rate of accumulation during the 1990s was much higher than that between 1959 and 1989, despite implementation of ballast water controls in 1989.

Approximately 70% of the NIS that established in the Great Lakes since the mid-1980s are native to the Black Sea basin (Ricciardi and MacIsaac 2000, MacIsaac et al. 2001). Ongoing invasions of key ports on the North Sea (e.g., Rotterdam, Antwerp) and the southern coast of the Baltic Sea by species native to the Black Sea basin 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 some species (e.g., the quagga mussel) appear to have been introduced by ships entering directly from a port on the Black Sea (Therriault et al. 2004).

Between 1981 and 2000, nearly three-quarters of the

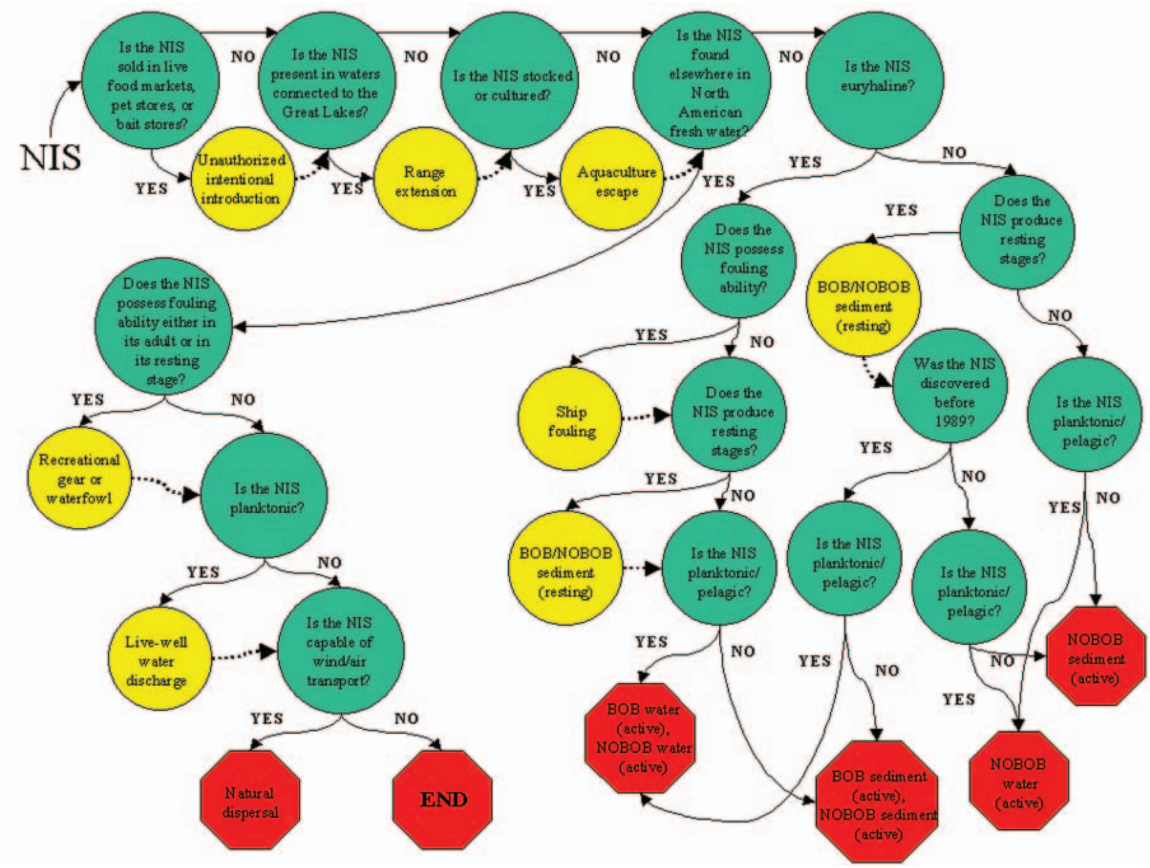

Figure 6. Vector assignment protocol used to determine the vectors by which faunal nonindigenous species (NIS) have been introduced to the Great Lakes since 1959. Moving through the flowchart, species are assigned one or more entry vectors until they reach an end point (red octagons). Entry vectors are described in box 1.

BOB vessels entering US ports on the Great Lakes proceeded directly to Lake Superior, and only on rare occasions did these ships not discharge their ballast there. In contrast, approximately 72% of NOBOB vessels made their first US port stop on Lake Erie, where they unloaded part of their cargo and took on ballast in preparation for travel to their next port. Both this mixed ballast water and the ballast water from BOB ships were discharged into Lakes Superior, Erie, Michigan, and St. Clair, in decreasing order of importance (figure 4). Ports on Lake Superior received more than 70% of the water from both BOB and NOBOB ships (figure 4). Based on this ballast discharge pattern, one might expect Lake Superior to be an invasion hotspot and to sustain the greatest number of NIS.

An analysis of the site where NIS were first described in the Great Lakes reveals that the St. Clair–Detroit River ecosystem, including southern Lake Huron and western Lake Erie, has been a particularly important area for establishment of NIS (10 species) since 1959. The western flank of Lake Superior, mainly around the port of Duluth-Superior, had seven recognized invasions, and the waters connecting Lakes Erie and Ontario had four. The St. Mary's River, which connects Lake Superior and Lake Huron, had two recognized initial invasions. Collectively, these invasion hotspots represent less than 6% of the Great Lakes' water surface but 54% of the NIS recorded there since 1959 (Grigorovich et al. 2003a). It is unclear what mechanisms are responsible for this pattern, but a number of possibilities exist. First, investigator bias could account for the pattern, since most researchers in the Great Lakes work on coastal areas along the lower lakes or western Lake Superior. However, a systematic study of habitats around the perimeter of Lake Superior failed to detect large numbers of new NIS, even though this lake has the largest exposure to ballast water (Grigorovich et al. 2003b). It is more likely that species establish in connecting channels owing to one or more of the following: the unreported (but legal) discharge of ballast water in shallow channels to reduce draft (ASI 1996); population "focusing" due to the relatively smaller water volume in these channels and reduced ship velocity; and the greater diversity of lentic and lotic habitats in these waters, providing more opportunities for species to establish than in a lake habitat.

The report rate of faunal NIS invasion attributed to shipping has increased since the voluntary ballast exchange guidelines went into effect in 1989 (figure 5). In fact, the annual rate from 1989 to 2000 was more than double that observed between 1959 and 1988. Investigator bias could partly account

Table 1. Entry vectors of faunal aquatic nonindigenous species reported in the Great Lakes basin from the opening of the St. Lawrence Seaway in 1959 through 1999, listed by year of first discovery.

Species	Common name	Year of discovery	Entry vector
Pisidium supinum	Humpback pea clam	1959	NOBOB sediment (active)
Lepisosteus platostomus	Shortnose gar	1962	Range extension
Eriocheir sinensis[a]	Chinese mitten crab	1965	BOB sediment (active) NOBOB sediment (active)
Bosmina coregoni	Cladoceran	1966	BOB water (active) NOBOB water (active) BOB/NOBOB sediment (resting)
Skistodiaptomus pallidus	Calanoid copepod	1967	Live well water discharge
Dugesia polychroa	Flatworm	1968	NOBOB sediment (active) Natural dispersal
Cyclops strenuus	Cyclopoid copepod	1972	Range extension Recreational gear or waterfowl Live well water discharge Natural dispersal
Nitocra hibernica	Harpacticoid copepod	1973	BOB sediment (active) NOBOB water (active) BOB/NOBOB sediment (resting)
Platichthys flesus[a]	European flounder	1974	BOB water (active) NOBOB water (active)
Notropis buchanani	Ghost shiner	1979	Unauthorized intentional introduction
Corbicula fluminea	Asiatic clam	1980	BOB sediment (active) NOBOB sediment (active)
Ripistes parasita	Oligochaete	1980	NOBOB sediment (active)
Alosa aestivalis	Blueback herring	1981	Range extension
Gianius aquaedulcis	Oligochaete	1983	NOBOB sediment (active)
Bythotrephes longimanus	Spiny water flea	1984	BOB water (active) NOBOB water (active) BOB/NOBOB sediment (resting)
Apeltes quadracus	Fourspine stickleback	1986	BOB water (active) NOBOB water (active)
Gymnocephalus cernuus	Eurasian ruffe	1986	BOB water (active) NOBOB water (active)
Bosmina maritima	Cladoceran	Before 1988	BOB water (active) NOBOB water (active) BOB/NOBOB sediment (resting)
Dreissena polymorpha	Zebra mussel	1988	Ship fouling BOB sediment (active) NOBOB sediment (active) BOB water (active) NOBOB water (active)

(continued)

for the elevated rate of invasion during the 1990s, since the issue of NIS invasion has received considerably more attention in recent years. Similarly, time lags may occur between establishment and initial reports of new NIS in ecosystems. The nature of these lags is not well understood, but it seems reasonable to assume that small and poorly studied taxa are less likely to be detected than macrofauna such as fish. If this increase in invasion rate is real, it may reflect changes in ship practices, trade routes, or species present in donor regions. These factors, individually or in combination, could result in changes to invasion risk (Carlton 1996, Ruiz and Carlton 2003).

Alternative vectors

Because a disproportionate number of NIS introductions are consistent with the ship vector, other vectors have received considerably less attention. Nevertheless, some recent studies suggest that nonship vectors are highly important in transmitting invasive species (e.g., aquarium releases in Florida; Padilla and Williams 2004). Some of the species transported to the Great Lakes by alternative vectors are demonstrably or potentially disruptive. For example, two of the more notorious NIS in the Great Lakes, sea lamprey (*Petromyzon marinus*) and alewife (*Alosa pseudoharengus*), are fishes that entered the system through man-made canals (Mills et al. 1993). Tremendous effort and expense are being devoted to preventing the introduction of two Asian fishes—the bighead carp (*Hypophthalmichthys nobilis,* also called *Aristichthys nobilis*) and the silver carp (*Hypophthalmichthys molitrix*)—through the Chicago Sanitary and Ship Canal (Stokstad 2003). This canal, which links the Mississippi River with Lake Michigan, presents a direct and potentially strong

Table 1. (continued)

Species	Common name	Year of discovery	Entry vector
Alosa chrysochloris[a]	Skipjack herring	1989	Range extension
Scardinius erythrophthalmus	Eurasian rudd	1989	Unauthorized intentional introduction
Dreissena bugensis	Quagga mussel	1989	Ship fouling BOB sediment (active) NOBOB sediment (active) BOB water (active) NOBOB water (active)
Neogobius melanostomus	Round goby	1990	BOB water (active) NOBOB water (active)
Proterorhinus marmoratus	Tubenose goby	1990	BOB water (active) NOBOB water (active)
Potamopyrgus antipodarum	New Zealand mud snail	1991	BOB sediment (active) NOBOB sediment (active)
Onychocamptus mohammed	Harpacticoid copepod	1992	BOB sediment (active) NOBOB sediment (active) BOB/NOBOB sediment (resting)
Echinogammarus ischnus	Gammarid amphipod	1995	BOB sediment (active) NOBOB sediment (active)
Heteropsyllus cf. nunni	Harpacticoid copepod	1996	BOB sediment (active) NOBOB sediment (active) BOB/NOBOB sediment (resting)
Cercopagis pengoi	Fishhook water flea	1998	Ship fouling BOB water (active) NOBOB water (active) BOB/NOBOB sediment (resting)
Schizopera borutzkyi	Harpacticoid copepod	1998	BOB sediment (active) NOBOB sediment (active) BOB/NOBOB sediment (resting)
Daphnia lumholtzi	Cladoceran	1999	Recreational gear or waterfowl Live well water discharge Natural dispersal
Nitocra incerta	Harpacticoid copepod	1999	BOB sediment (active) NOBOB sediment (active) BOB/NOBOB sediment (resting)

BOB, ballast on board (ships carrying ballast water and sediment); NOBOB, no ballast on board (ships carrying cargo, with residual water and sediment).
Note: "Active" indicates an active life stage (e.g., free-swimming adults); "resting" indicates a resting life stage (e.g., eggs). Parasites introduced with their host species are not included.
a. Reported in the Great Lakes, but not thought to have established a reproducing population.

Table 2. Some aquatic faunal species posing a high invasion risk to the Great Lakes basin.

Species	Common name	Potential entry vectors
Aristichthys nobilis[a]	Bighead carp	Unauthorized intentional introduction Range extension Aquaculture escape
Clupeonella caspia[b, c]	Tyulka, Caspian kilka	BOB water (active) NOBOB water (active)
Corophium curvispinum[b]	Amphipod	BOB sediment (active) NOBOB sediment (active)
Neogobius fluviatilis[b, c]	Monkey goby	BOB water (active) NOBOB water (active)

BOB, ballast on board (ships carrying ballast water); NOBOB, no ballast on board (ships carrying cargo, with residual water).

Note: "Active" indicates an active life stage (e.g., free-swimming adults); "resting" indicates a resting life stage (e.g., eggs).

Source: a, Rixon and colleagues (2004); b, Ricciardi and Rasmussen (1998); c, Kolar and Lodge (2002).

vector for invasion. Bighead carp are also sold live in Asian food markets in the Great Lakes basin (Kolar and Lodge 2002, Duggan et al. 2003, Rixon et al. 2004), although recent legislation in Ontario prohibits the live sale of these fish. Other possible vectors of NIS to the Great Lakes include the escape or release of live species reared in aquaculture operations and sold in retail pet, aquarium, or baitfish stores (see discussion in Duggan et al. 2003, Rixon et al. 2004). Rixon and colleagues (2004) identified two aquarium fishes (*Misgurnus anguillicaudatus, Tanichthys albonubes*), three aquarium plants (*Hydrophila polysperma, Myriophyllum aquaticum, Egeria densa*), and two live food fishes (*Hypophthalmichthys nobilis, Ctenopharyngodon idellus*) as species that could invade the Great Lakes through live fish markets or the aquarium trade. Kolar and Lodge (2002) identified four fishes that may become established in the Great Lakes through vectors other than shipping and projected that one of these species could attain nuisance status. Thus, even if the problems of ship vectors are resolved, alternative vectors could still deliver invasive species to the Great Lakes.

Box 1. Vectors of introduction for aquatic nonindigenous species in the Great Lakes.

These categories describe the end points of the vector assignment protocol (figure 6) used in this study of faunal species introductions in the Great Lakes. Parasites introduced with their host species are not included.

Unauthorized intentional introduction: Possible unauthorized intentional introduction (e.g., release of aquarium or bait fish) without intent to create an established population.

Range extension: Possible introduction by passive or active movement from an infected area (e.g., through man-made canals).

Aquaculture escape: Possible unintentional introduction by escape from aquaculture.

Recreational gear or waterfowl: Possible introduction fouled to a boat, boat trailer, fishing line, anchor line, or waterfowl.

Live well water discharge: Possible introduction through discharge from live wells or through recreational gear containing residual water (e.g., boat pontoons, scuba gear).

Natural dispersal: Possible introduction by a natural vector (e.g., wind, rain).

Ship fouling: Possible introduction by external fouling on a ship, either with ballast on board (BOB) or no ballast on board (NOBOB).

BOB water (active): Possible introduction live (during an active life stage) in ballast water from BOB ships.

BOB sediment (active): Possible introduction live in sediment from BOB ships.

NOBOB water (active): Possible introduction live in residual ballast water from NOBOB ships.

NOBOB sediment (active): Possible introduction live in sediment from NOBOB ships.

BOB/NOBOB sediment (resting): Possible introduction through resting stages in the sediment of BOB or NOBOB ships.

Figure 7. The amphipod **Corophium curvispinum** *(top) and the monkey goby,* **Neogobius fluviatilis** *(bottom), two species that pose a high risk of invading the Great Lakes through the ship vector. Photographs: top, Henry M. Reiswig and Anthony Ricciardi; bottom, Zoltán Sallai.*

Understanding links between NIS and vectors

Attempting to forecast introductions and their related entry vectors is an important step toward developing useful strategies for vector management. In the Great Lakes, for example, the ecological and economic costs associated with NIS, and the importance of ships as a primary vector, dictate the necessity of evaluating the effectiveness of current ballast management practices and better characterizing the ship vector. To facilitate prediction of high-risk species from the Ponto-Caspian region that could enter the Great Lakes through the ship vector, Ricciardi and Rasmussen (1998) described an approach that aligns the characteristics of the donor region with biological characteristics of species that have invasion histories elsewhere. Drawing on the work of Carlton (1996), Grigorovich and colleagues (2003a) used species' invasion histories, physicochemical attributes, and life-history characteristics, along with shipping traffic patterns, to identify taxa that are likely to survive transport via the ship vector. Similarly, Kolar and Lodge (2002) used life-history characteristics and probable donor regions to forecast possible fish invaders of the Great Lakes.

Vectors for species introduction are often identifed on the basis of a small number of criteria, and often without consideration of other possible vectors. Here we present a vector assignment protocol (VAP; figure 6) that uses information gleaned from prior invasions of the Great Lakes to classify entry vectors for faunal NIS reported in the system since 1959 (table 1). For those species that entered through the ship vector, the VAP further refines the entry mechanism (fouling; ballast water or sediment in BOB ships; residual ballast water or sediment in NOBOB ships). For example, possible end points (box 1) for the introduction of the zebra mussel through the ship vector include fouling, sediment or residual water in NOBOB vessels, and sediment or ballast water in BOB vessels. Because this mollusk was discovered before the implementation of ballast water exchange policies, it is possible that it was introduced through BOB ballast water; at that time, ballasted vessels were not required to perform open-ocean exchange and therefore contained water from their penultimate port of call. *Cercopagis pengoi,* a water flea discovered in Lake Ontario in 1998 (MacIsaac et al. 1999)—well after ballast water regulations took effect—may have been introduced through many of the submechanisms related to the ship vector: live in a NOBOB ship's ballast water, as a resting stage in a NOBOB ship's sediment, live in a BOB ship's ballast water (owing to its salinity tolerance), as a resting stage in a BOB ship's ballast sediment, or as a fouling organism on a ship's hull or anchor lock. *Cercopagis* spread rapidly to Lakes Michigan and Erie and to the inland waters in the Finger Lakes region of upstate New York. Generally, species that possess biphasic life modes such as planktonic larvae and biofouling, sedentary adults (e.g., zebra mussels), or that have active and dormant phases (e.g., *Vibrio cholerae* bacteria or *Cercopagis* water fleas), may be capable of exploiting many different dispersal vectors, and consequently may be represented frequently among introduced NIS. These species may also pose the greatest problem to managers attempting to curtail subsequent secondary spread, since dispersal may be affected by so many unrelated mechanisms.

The ability to forecast introductions could provide the basis for preventing future invasions. Predictive risk assessments have been attempted for invasive aquatic species in general (Carlton et al. 1995, Hayes 1998, MacIsaac 1999), for particular taxa such as fish (Kolar and Lodge 2002, Rixon et al. 2004), and for species that inhabit particular donor regions (Ricciardi and Rasmussen 1998). Although not a predictive model, the VAP can be used to assess the entry mechanisms of future invaders (table 2), and it may prove useful to managers attempting to identify and eliminate specific vectors of introduction. For example, two Ponto-Caspian species that have been assessed as high-risk for invasion of the Great Lakes through the ship vector are the amphipod *Corophium curvispinum* and a fish, the monkey goby (*Neogobius fluviatilis*) (figure 7; Ricciardi and Rasmussen 1998, Kolar and Lodge 2002). Using the VAP, we can explore which mechanisms these potential NIS are most likely to exploit. For example, *Co. curvispinum* could arrive live in BOB or NOBOB ballast sediment, and *N. fluviatilis* could enter in BOB water or NOBOB residual water. The use of the VAP to evaluate potential invaders can provide a focal point for efforts to prevent invasions from occuring through the various submechanisms of the ship vector. Furthermore, the VAP can be used to systematically elucidate the entry vector for any NIS that establishes in the Great Lakes, and can be modified for different ecosystems according to the vectors operationally specific to those sites.

Discussion

Alignment of high-risk NIS with probable entry vectors is a step toward the prevention of future invasions. This is particularly important in the Great Lakes, because recent evidence suggests that the system may have entered an "invasional meltdown" phase (Ricciardi 2001). Facilitations between invaders have resulted in synergistic effects, causing serious alterations to key ecosystem processes. For example, during the mid-20th century, overfishing and predation by the nonnative sea lamprey decimated populations of lake trout (*Salvelinus namaycush*) in the upper Great Lakes (Eshenroder and Amatangelo 2002). The loss of lake trout facilitated the invasion success of another NIS: the alewife, a species that the trout preferred as prey. Massive populations of alewife competed with native planktivores, resulting in an overall decline in fishery productivity (Smith 1970). Zebra mussels, another invasive species in the Great Lakes, have facilitated the invasion of two coevolved species—an amphipod (*Echinogammarus ischnus*) and a predatory fish (the round goby, or *Neogobius melanostomus*)—by providing complex physical habitat and food, respectively (Ricciardi 2001, van Overdijk et al. 2003). The biomass of *Ec. ischnus* increased 20-fold in areas of western Lake Erie where zebra mussels had established (Stewart et al. 1998), and *Ec. ischnus* has partly supplanted other amphipods (e.g., *Gammarus fasciatus*) in zebra mussel beds in Lake Erie and Lake Ontario (Dermott et al. 1998, van Overdijk et al. 2003). An unpredicted synergistic effect, the recurrent outbreak of type E botulism in Lakes Erie and Ontario, has resulted in the deaths of tens of thousands of waterfowl, primarily scavenging gulls and fish-eating loons and mergansers. Botulin toxin—produced by the bacteria *Clostridium botulinum*—accumulates in the tissue of these birds when they ingest fish, such as round goby, whose diets consist primarily of zebra mussels. Not only do dreissenid mussels concentrate the toxin as they filter water proximal to the sediments that contain the *Clostridium* bacteria, they also generate large amounts of fecal deposits that may contribute to the anoxic conditions favoring the proliferation of *Clostridium.*

These examples demonstrate that previous introductions can facilitate the introduction and success of subsequent arrivals. Together, NIS can leverage each other's impacts, creating synergistic disruptions. Therefore, halting the introduction of any one NIS (e.g., through control of ballast water discharge and other vectors) could prevent disproportionate harm to the ecosystem by inhibiting a potentially large number of other invaders whose success and impact are magnified by that species. Efforts to halt the influx of NIS to the Great Lakes and other large aquatic ecosystems must consider transoceanic shipping, which remains the largest source of NIS in the Great Lakes.

The Great Lakes ballast water regulations raised hope for greatly diminishing the risk of future NIS invasions through the ship vector. Unfortunately, ship-mediated invasions of the Great Lakes appear to have increased rather than decreased since implementation of this management strategy (Ricciardi 2001, Grigorovich et al. 2003a). The present rate of discovery of new NIS in the Great Lakes exceeds the level observed in earlier years, which, together with the increasing frequency of facilitations between invaders, supports the idea that the system may have entered a phase of invasional meltdown (Ricciardi 2001). Management strategies aimed at preventing new invasions must consider the linkages between NIS and vectors. Without means of prevention and control to reduce NIS introduced by ships and other, emerging vectors, we can expect the number of NIS in the Great Lakes to continue to rise, with an associated loss of native biodiversity and an increase in unpredicted ecological disruptions.

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