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# The future of species invasions in the Great Lakes-St. Lawrence River basin

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ABSTRACT

No other freshwater system contains as many non-native species or has been invaded as frequently as the Great Lakes-St. Lawrence River basin. Over 180 non-native species have become established in the basin within the past two centuries. Collectively, these invasions have altered biodiversity, habitat structure, productivity, water quality, contaminant cycling and ecosystem services. The composition and rate of discovery of invaders are correlated with changes in dominant vectors, such as transoceanic shipping. We review the invasion history of the basin and identify future invasion threats by considering trends and potential scenarios in changing vectors and pathways. Whereas most non-native species discovered since the opening of the St. Lawrence Seaway in 1959 were attributable to ballast water discharge from transoceanic vessels, recent regulations have apparently reduced the threat of this vector. Nevertheless, non-native species may continue to be introduced through poorly-regulated vectors, particularly those associated with trade in live organisms. The spread and impact of current and future invaders are expected to be exacerbated by interactions with other anthropogenic stressors that are increasing in frequency and spatial extent. Most notably, the continued warming of surface waters of the Great Lakes basin will lift thermal barriers to invasions by warm-water taxa. Contrary to any perception that the "worst is over" (i.e. most harmful invasions have already occurred), the basin remains vulnerable to further ecological and economic disruptions from non-native species.


## Introduction

The Great Lakes-St. Lawrence River basin (hereafter, the Great Lakes basin) is the world's most invaded freshwater system (Ricciardi, 2006). Non-native species have been introduced to the basin through numerous vectors and pathways that operate on multiple spatial scales and are mediated by environmental and socioeconomic factors (Mills et al., 1993, 1994; Ricciardi, 2006). The relative influence of a given vector or pathway evolves as new regulations are implemented and the recipient ecosystem is altered by various stressors (Williams et al., 2013). Therefore, a strategy to address the scope of challenges presented by invasive species (defined here as those non-native species that spread aggressively and cause undesirable impacts) must involve managing vectors, developing risk assessments, monitoring for new non-native populations, and implementing appropriate policy — all in the context of shifting patterns of invasion risk. To this end, resource managers require knowledge of changes in vector activity, the efficacy of current regulations and control strategies, and future invasion threats.

Valuable predictive information can be derived from an analysis of invasion history and vector activity within the Great Lakes basin. Here, we examine patterns of species introductions in the basin over the past 50 years (1963–2013), with consideration given to other drivers including climate change and legislative actions. We then hypothesize three scenarios for the basin over the next 50 years (2013–2063), based on 1) the effectiveness of different governance strategies that have been, or may be, adopted for regulating currently active vectors

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and pathways, and 2) projected rates of warming of surface waters. Under each scenario, we identify probable future invaders entering the Great Lakes basin using a simple algorithm.

## A long history of species invasions in the Great Lakes Basin

Over 180 non-native species have been recorded established in the Great Lakes basin within the past two centuries (GLANSIS, 2014; Mills et al., 1993; Ricciardi, 2006). About 40% of these species were introduced via shipping (i.e., ballast water release, dumping of solid ballast, and hull fouling). Ship-mediated invasions have grown in frequency over the past 50 years (Fig. 1), concomitantly with increased visits and greater volumes of ballast water discharged by transoceanic vessels entering the basin since the opening of the St. Lawrence Seaway in 1959 (Ricciardi, 2006). In contrast, hull fouling associated with international shipping has played an unimportant role (likely responsible for only two species introductions – both involving marine algae; Ricciardi, 2006), because of the lack of environmental match between transported species and recipient freshwater habitats (Sylvester and MacIsaac, 2010). Another source of introductions that has grown in recent decades are vectors involving 'live trade' – the commercial importation of live organisms (e.g., ornamental plants, aquarium pets, baitfish, fish and invertebrates for food markets, organisms for scientific research and teaching). Most non-native fish present in the Great Lakes basin were delivered to the region through commercial sale as food, live bait, or stocking for angling and aquaculture (Mandrak and Cudmore, 2010). Some plant and animal invasions have apparently resulted from unauthorized aquarium releases (Mills et al., 1993), which are

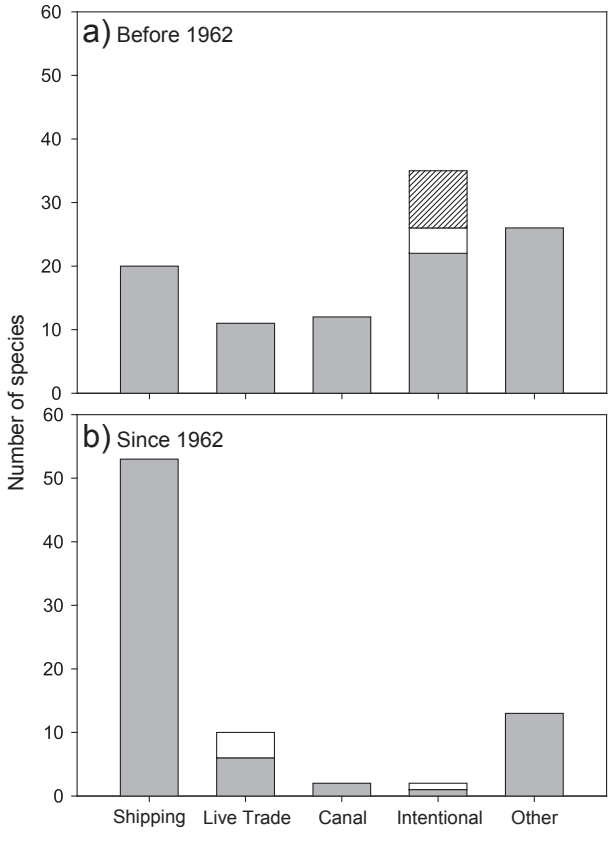


**Fig. 1.** The number of established non-native species in the Great Lakes distinguished by vector of entry, before and after 1962. 'Shipping' constitutes all activities related to this vector (ballast water, solid ballast, hull fouling), 'Live Trade' includes aquarium/ornamental/pet releases (gray) and bait fish releases (white), whereas 'Intentional' refers to stocked fish (gray) and cultivated plants (white), as well as other methods of intentional release (crosshatched). Data are from Mills et al. (1993), Ricciardi (2006) and GLANSIS (2014).

frequent and involve a diverse range of taxa (Cohen et al., 2007; Leach, 2003). By comparison with shipping and live trade vectors, canals have become less influential as a source of primary introductions in the latter part of the 20th century (Fig. 1), but remain an important vector of secondary spread for species already established in the basin, and may also play an important role in facilitating new invasions mediated by climate change (see *Canals and recreational boating*).

Nearly half of all non-native species recorded as established in the Great Lakes basin are Eurasian, and most of these were introduced either intentionally or through shipping vectors (Fig. 2). In recent decades, ship-mediated invasions have often involved Ponto-Caspian species — i.e. those originating from the freshwater and brackish margins of the Azov, Black, and Caspian Seas (Ricciardi and MacIsaac, 2000). Invasions associated with live trade most often involve Asian and Eurasian species. Species from a variety of regions have invaded the Great Lakes basin through canals, but the majority is indigenous to the Atlantic and Mississippi drainages (Fig. 2).

Since the opening of the Seaway, one new established non-native species has been discovered every 8 months (82 species since 1960), or 1.52/year, on average (Ricciardi, 2006; Ricciardi, unpubl. data). This well exceeds rates recorded for the Rhine River (0.56/yr; Leuven et al., 2009), the Hudson River (0.66/yr; Mills et al., 1997), Lake Champlain (0.68/yr; Marsden and Hauser, 2009), the Columbia River (0.84/yr; Sytsma et al., 2004) and the Thames River (1.04/yr; Jackson and Grey, 2012). The number of new discoveries peaked between 1959 and 1993, which was a period characterized both by high shipping frequency and unregulated ballast water release. Ballast water carried by ships arriving from foreign ports was regulated for the first time in 1993 and more comprehensively in 2006 (GC, 2006). Virtually all ships entering the seaway since 2008 were inspected for compliance (GLSBWWG, 2014). Perhaps as a result, the number of non-native species discovered in the 2000s is the lowest for any decade since the Second World War. Indeed, no new invasions attributable to shipping have been reported since 2006 (Bailey et al., 2011).

### *Impacts of species invasions in the Great Lakes basin*

The impacts of most non-native species in the Great Lakes basin are poorly known (Mills et al., 1993). Nevertheless, non-native species have been shown to be a driving force of ecological change within the basin, causing native biodiversity declines, food web transformations, altered nutrient and contaminant cycling, and shifts in productivity (Hogan et al., 2007; Mills et al., 1993; Ricciardi, 2001; Vanderploeg et al., 2002). A prominent example is the sea lamprey *Petromyzon marinus*, which spread quickly throughout the Great Lakes basin and contributed to the collapse of native lake trout *Salvelinus namaycush* populations in the late 1940s and 1950s (Mills et al., 1993). Within two decades, the annual commercial yield of lake trout was reduced from 15 million pounds to only 300 000 pounds in the upper Great Lakes, whereas in the lower Great Lakes the lake trout fishery disappeared by 1960 (GLFC, 2010). The loss of this top predator facilitated the expansion of populations of alewife *Alosa pseudoharengus* in the 1950s and 1960s (Ricciardi, 2001), which provoked the declines of native planktivorous fishes (Mills et al., 1994).

High-impact invaders appear to have become more frequent in recent decades (Table 1), but it is not clear whether this trend reflects a reduction in the resilience of ecosystems in the Great Lakes basin or an artifact of better detection methods and increased scientific attention to ecological change. Nearly 20% of all invading species discovered over the past 50 years have had significant impacts on native species populations (Ricciardi, unpubl. data). For example, the Eurasian ruffe *Gymnocephalus cernuus* and the round goby *Neogobius melanostomus* have displaced native fishes (Balshine et al., 2005; Lauer et al., 2004), and predatory waterfleas *Bythotrephes longimanus* and *Cercopagis pengoi* have drastically altered zooplankton communities (Barbiero and Tuchman, 2004a). A variety of introduced pathogens have caused