Received: 22 August 2021 | Revised: 12 December 2021 | Accepted: 16 December 2021

DOI: 10.1111/conl.12866

LETTER

Conservation Letters
A journal of the Society for Conservation Biology
Open Access
WILEY

Vector control reduces the rate of species invasion in the world's largest freshwater ecosystem

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Funding information
Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: NSERC RGPIN/03918-2016

Abstract

The Great Lakes-St Lawrence River basin is the world's most invaded freshwater system. Ballast water release from transoceanic shipping is deemed responsible for 65% of invasions in the basin since the modern St. Lawrence Seaway opened in 1959. Regulations requiring mid-ocean exchange of ballast water applied in 1993 failed to stem ship-mediated invasions because the procedure was not mandated for all ships. In 2006 and 2008, Canada and the United States, respectively, mandated that all transoceanic ships should conduct open ocean flushing to ensure that partially filled ballast tanks intended for discharge into the Great Lakes contained water of salinity ≥30 ppt before entering the Seaway. These regulations have been strictly enforced through record inspections and tests of ballast tank salinities of inbound ships. Before-and-after comparisons of total organismal abundance and species richness in ballast tanks revealed a substantial reduction in invasion risk from ships that conducted saltwater flushing. Since 2006, the rate of discovery of newly established non-native species in the Great Lakes declined by 85% to its lowest level in two centuries. While multiple factors could plausibly contribute to this decline, empirical evidence supports the 2006/2008 ballast water regulation as the primary cause, highlighting the benefit of internationally coordinated vector control.

KEYWORDS

ballast water, biological invasion, Great Lakes, invasion rate, non-native species, transboundary management, transoceanic shipping

1 | INTRODUCTION

Under human influence, species are spreading faster, farther, and in greater numbers beyond their natural ranges than ever before (Ricciardi, 2007; Seebens et al., 2017). Biological invasions threaten biodiversity, ecosystem services, and regional economies, thus posing an enormous global challenge to conservation and resource management (Blackburn et al., 2019; Diagne et al., 2021; Pyšek et al., 2020). They constitute a "wicked problem"—defined as having complex cause-and-effect relationships between the entities involved, whose solutions require collaboration among multiple stakeholders to determine appropriate actions (Woodford et al., 2016). The chronic costs of managing established invasive species are not sustainable, given that global invasion rates show no sign of saturation (Seebens et al., 2017, 2018). Attempts to eradicate or contain the spread of newly established invasive species populations have had mixed success worldwide (e.g., Simberloff, 2021); therefore, the most cost-effective management strategy is to reduce risks of invasion by controlling key vectors of species introduction (e.g., Vander Zanden et al., 2010). The ultimate efficacy of a vector control strategy can be evaluated by comparing observed patterns and rates of invasive species discovery (the best available proxy for the invasion rate) before and after the strategy's implementation, assuming time lags between species arrival and reporting remain constant. Here, we evaluate evidence that a binational management intervention to regulate ballast water discharge from inbound transoceanic ships is the primary cause of a dramatic reduction in the apparent invasion rate for the world's largest freshwater ecosystem, the Great Lakes-St. Lawrence River basin (hereafter "the Great Lakes basin").

The invasion history of the Great Lakes basin spans two centuries and involves a broad array of vectors including shipping, canals, aquarium release, bait release, aquaculture escapes, and intentional stocking, whose relative influence has varied through time (Mills et al., 1993; Ricciardi, 2006; Sturtevant et al., 2019). The impacts of the vast majority of the circa 190 nonnative species established in the Great Lakes basin are undocumented, but at least 30% of these invaders are known to have had measurable negative ecological and/or socioeconomic impacts (Sturtevant et al., 2019)—and for at least one-third of this subset, impacts are moderate to enormous (Mills et al., 1993; Ricciardi, 2001, 2006; Sturtevant et al., 2019) and include major changes to biodiversity, fisheries, and ecosystem function. Aquatic invasive species have long been considered a dominant environmental stressor and a high-priority management problem for the basin (Allan et al., 2013; Rothlisberger et al., 2012). Between 1959 and 2006 inclusive, 82 non-native species were discovered established in the Great Lakes basin, from which one can infer an invasion rate of 1.71 species per year, the highest recorded for any freshwater ecosystem (Ricciardi, 2006).

It can be challenging to ascribe an introduction vector for individual species when multiple possibilities exist; however, it is possible to identify the most likely vector of introduction based on the biological attributes of the species and its invasion history (Mills et al., 1993). Furthermore, although time lags between the introduction of a species, its initial discovery, and formal reporting renders temporal analyses of invasion rates difficult (Crooks, 2005), much of the variation in the numbers and composition of invaders discovered over time in the Great Lakes can be explained by historical changes in the dominant vectors operating in the basin (Ricciardi, 2006), suggesting a strong link between vector activity and invasion risk.

1.1 | The role of ballast water release

Large volumes of ballast water are taken up at source ports by ocean ships lacking cargo so that the ships can regulate stability and trim. This water can contain diverse organisms ranging from microbes to fish (Carlton & Geller, 1993; Chan et al., 2015; Huang et al., 2018), which are later discharged at one or more destination ports (e.g., Colautti et al., 2003). Within a global shipping network that connects disparate regions of the world, thousands of species are being transported in ballast tanks at any given moment (Carlton, 1999; Keller et al., 2011; Seebens et al., 2013). Thus, ballast water release is a dominant invasion vector for marine, estuarine, and large inland aquatic ecosystems worldwide (Endresen et al., 2004; Molnar et al., 2008). Transoceanic ships accessed the Great Lakes via the St. Lawrence canal system after 1847, and ballast water could have been released into the Great Lakes by the 1880s (Mills et al., 1993). The opening of the enlarged St. Lawrence Seaway in 1959 allowed a higher frequency and larger size of ships to transit the basin. In subsequent decades, twice as many tonnes of cargo were exported from the basin than were imported (GLSLSS, 2021), indicating that the Great Lakes became a net importer of ballast water. Since 1959, the majority (~65%) of invasions recorded in the Great Lakes basin are attributable to ballast water release by transoceanic ships (NOAA, 2021; Ricciardi, 2006); in contrast, biofouling of ships' hulls has likely accounted for only two (~1%) invasions over the past 2 centuries, owing to negative effects of exposure to marine salinities (Mills et al., 1993).

Following prominent ship-mediated invasions by Eurasian species including the spiny waterflea (*Bythotrephes longimanus*), the ruffe (*Gymnocephalus cernuus*), and the zebra mussel (*Dreissena polymorpha*), transoceanic ships with filled ballast tanks were requested by Canada in 1989 (Canadian Coast Guard, 1989) and then mandated by the United States in 1993 (USCG, 1993) to exchange their freshwater or estuarine ballast with oceanic water prior to entering the Great Lakes, a procedure termed "mid-ocean ballast water exchange." Under this procedure, it was expected that freshwater organisms in ballast tanks would be purged or, if they remained among the tank sediments, killed by highly saline water, thereby severely reducing the number of introduced individuals (propagule pressure *sensu* Lockwood et al., 2005) and taxa (colonization pressure *sensu* Lockwood et al., 2009).

It was subsequently determined that 75%–95% of ships visiting the Great Lakes were loaded with cargo and declared no pumpable ballast on board ("NOBOB ships"), thus exempting them from this regulation even though they carried residual water that would be discharged into the Great Lakes (Colautti et al., 2003; Holeck et al., 2004). Diverse taxa with broad tolerance or resistant dormant stages reside in residual water and tank sediments, and resting eggs of several species retrieved from ballast tanks of NOBOB ships were viable and hatched successfully (Bailey et al., 2004; Bailey, Duggan, et al., 2005; Bailey, Nandakumar, et al., 2005; Duggan et al., 2005). Likely for these reasons, the regulation did not reduce the overall invasion rate (Ricciardi, 2006; Ricciardi & MacIsaac, 2008; Sturtevant et al., 2019). Invasions during the period following 1993 were dominated by taxa that could survive exposure to mixed salinities of residual ballast (Pauli & Briski, 2018; Ricciardi, 2006). Moreover, studies identified several potentially high-impact invaders with broad salinity tolerance that could invade the Great Lakes basin if the ballast water vector remained only partially regulated (MacIsaac et al., 2015; Pagnucco et al., 2015; Ricciardi & Rasmussen, 1998). One such species, the Ponto-Caspian mysid shrimp *Hemimysis anomala*, did become established in the Great Lakes by 2006 (Pothoven et al., 2007).

In June 2006, Canada enacted enhanced ballast water regulations mandating saltwater flushing as a treatment for NOBOB ships (Government of Canada, 2006), a policy followed in 2008 by the United States (Saint Lawrence Seaway Development Corporation, 2008). Saltwater flushing involves rinsing ballast tanks through the uptake and subsequent discharge of small amounts of open-ocean water, so as to purge most residual water while simultaneously achieving saline conditions (≥30 ppt) that will kill freshwater organisms through osmotic stress. Compliance with the new regulation was insured by inspection of ballast tank exchange records or examination of water salinity of tanks for each ship entering the Great Lakes by coordinated efforts of Canadian and American agencies. Typically, 96%–99% of ships entering the seaway are in compliance with the regulation (BWWG, 2019). Any tank that failed inspection was sealed and forbidden from discharge into the system.

Using reconstructed aquatic invasion histories to test for emergent patterns is a trusted methodology (e.g., Ricciardi, 2006; Ruiz et al., 2000) which we apply here to evaluate the 2006/2008 binational management intervention. Recognizing that at least several years of data are required to assess efforts to control the apparent rate of invasion (Costello & Solow, 2003), we examined the rate of discovery of established invaders as an indicator of the effectiveness of the 2006/2008 ballast water regulation in suppressing invasion risk in the Great Lakes basin.

2 | METHODS

We used a comprehensive database of non-native species of vascular plants, algae, invertebrates, and fishes recorded as established in the Great Lakes basin (including each of the Great Lakes and their drainages) from the year 1959 to 2019. For the purposes of this study, non-native species are those that have no recent evolutionary history in the basin; a species whose evolutionary origins are poorly known was considered non-native if it met at least three of the criteria described by Chapman and Carlton (1991), following the approach of Ricciardi (2006) and NOAA (2021). “Established” means that the species has likely formed a persistent, reproducing population.

Data for analyses were obtained from Mills et al. (1993), Ricciardi (2006), and NOAA (2021), as well as from literature searches using Web of Science that spanned the period from 1959 to 2020, inclusive. For each invader, we determined the year of its discovery and the most plausible vector of introduction, which were typically provided in the published report of its discovery or otherwise could be ascertained from regional databases and published reviews. Established non-native species and their year of discovery are the same as those listed in the online database the Great Lakes Aquatic Nonindigenous Species Information System (GLANSIS; NOAA, 2021), except for several revisions based on our own literature review (see explanations and dataset in Table S1). Invasion rates were estimated by dividing the number of established non-native species discovered over a given time interval by the length of that interval (Ricciardi, 2006). This calculation was done for three consecutive 13-year time periods, chosen as balanced intervals that encompass distinct regulatory practices: (i) 1981–1993, pre-regulation (mid-ocean ballast water exchange was voluntary in 1989 under Canadian guidelines, and subsequently mandated by the United States in April 1993); (ii) 1994–2006, partial regulation—when only fully ballasted ships were require to flush their tanks with saltwater prior to entry (partial regulation remained in effect until June 2006); and (iii) 2007–2019, total regulation—when all inbound ships were required to conduct saltwater flushing. Differences in the mean number of invaders found across all time periods were tested using a Poisson GLM with Tukey pairwise comparisons of means (R Core Team, 2018).

Annual numbers of ships entering the seaway to visit Great Lakes ports were obtained from ship traffic reports and historical tables prepared by the St. Lawrence Seaway Management Corporation and the Saint Lawrence Seaway Development Corporation for 1981–2019 (GLSLSS, 2021) and were used to compare shipping activity across

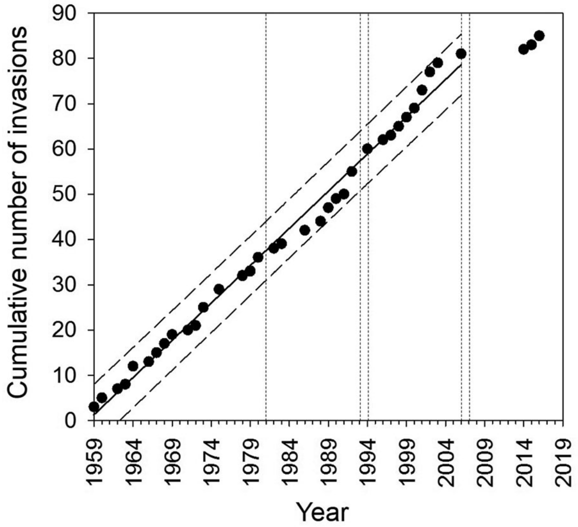

FIGURE 1 Cumulative number of invasions in the Great Lakes basin since 1959, including those attributable to vectors other than shipping. Trend line (1959–2006) fitted by least-squares regression: $y = 1.277x - 1.646$ ($R_{adj}^2 = 0.99$), where x is number of years since 1959. Dashed lines show 99% prediction band around the trend line. Vertical lines demarcate three 13-year time periods: 1981–1993, before any ballast water regulation; 1994–2006, partial regulation—when only fully ballasted ships were targeted; and 2007–2019, total regulation—when all vessels were regulated. See Table S1 for data

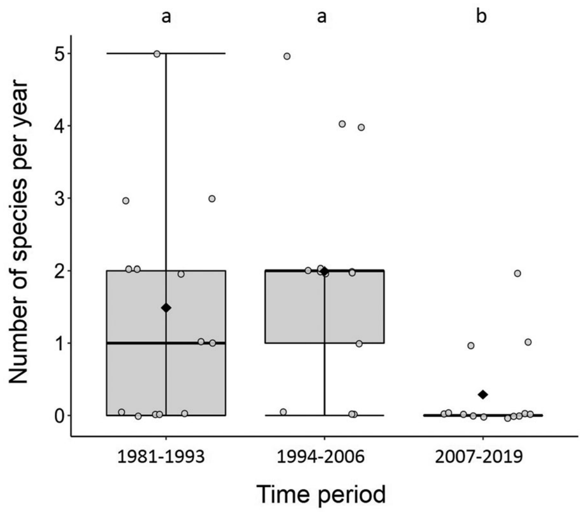

FIGURE 2 Box plot of numbers of invaders discovered in the Great Lakes basin each year in three 13-year time periods: 1981–1993, before any ballast water regulation; 1994–2006, partial regulation—when only fully ballasted ships were targeted; and 2007–2019, total regulation—when all ships were regulated. Note that 25th and 75th quartiles (lower and upper box hinges), medians (thick bars), and means (diamonds) are shown. Outer whiskers are 1.5× quartile range. Plots with distinct letters indicate differences between means ($p < 0.05$, Poisson GLM with Tukey pairwise comparisons). See Table S1 for data

the three time periods (Table S2). Additional information was obtained for 1995–2006 and 2007–2019 (Table S3) to assess whether numbers of inbound arrivals of ballasted ships and NOBOB ships using the Montreal to Lake Ontario segment of the seaway differed between these periods (two-sample *t*-tests with equal variance). To evaluate environmental differences among the time periods, mean annual and mean summer surface water temperature data for the three most invaded Great Lakes (Erie, Ontario, Michigan) in the years spanning 1995 to 2019 were obtained from NOAA Great Lakes Surface Environmental Analysis (https://coastwatch.glerl.noaa.gov/statistic/statistic.html). Trends in temperature data were evaluated using least-squares regression in Sigmaplot 14.5 (Systat Software Inc., San Jose, California). Mean annual temperatures for the periods of 1995–2006 and 2007–2019 were compared using one-tailed *t*-tests.

3 | RESULTS

Between 1959 and 2006, compiled data revealed a linear accumulation of invaders in the Great Lakes basin (Figure 1). This trend was evident even during partial regulation (1994–2006), but was disrupted thereafter. The invasion rate for the 13-year period prior to 1981 (24 species, 1.85/year) was higher—and the number of ship-mediated invaders (13 species, 1.0/year) was lower—than the subsequent period of 1981–1993. Numbers of invaders discovered in the pre-regulation (1981–1993) and partial regulation (1994–2006) periods (i.e., 19 and 26 species, respectively) are not significantly different (Poisson GLM, $Z = 1.039$, $p = 0.54$; Figure 2). However, numbers of invaders found in both these periods were significantly higher than the number (four species in total) discovered during the regulation period (1981–1993 vs. 2007–2019: $Z = -2.832$, $p = 0.0121$; 1994–2006 vs. 2007–2019: $Z = -3.485$, $p = 0.001$). The inferred rate of invasion increased from 1.46 to 2.0 species per year between the pre-regulation and partial regulation periods, and then fell by 85% to a rate of 0.31 species per year after total regulation was implemented. When we examine data for invasions attributed exclusively to ballast water release, the number of invaders discovered over the pre-regulation (1981–1993), partial regulation (1994–2006), and total regulation (2007–2019) periods was 16, 15, and 2 species, respectively, suggesting an 87% decline in ballast water invasions under total regulation.

Ship traffic varied across time periods, but not substantially (Figure 3). The mean annual number of ship visits for the pre-regulation (1981–1993), partial regulation (1994–2006), and total regulation (2007–2019) periods was 2379, 2130, and 2028, respectively. Multiple

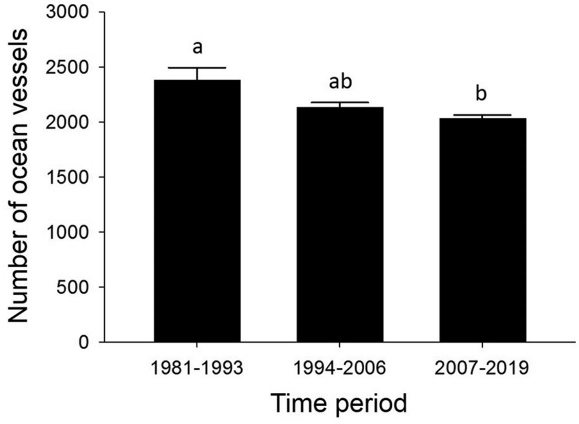

FIGURE 3 Mean (±1 standard error) number of visits by inbound ocean ships to the Great Lakes during three 13-year time periods: 1981–1993, before any ballast water regulation; 1994–2006, partial regulation—when only fully ballasted ships were targeted; and 2007–2019, total regulation—when all ships were regulated. Bars with distinct letters indicate differences between means ($p < 0.05$; pairwise comparisons with two-tailed t-tests). See Table S2 for data

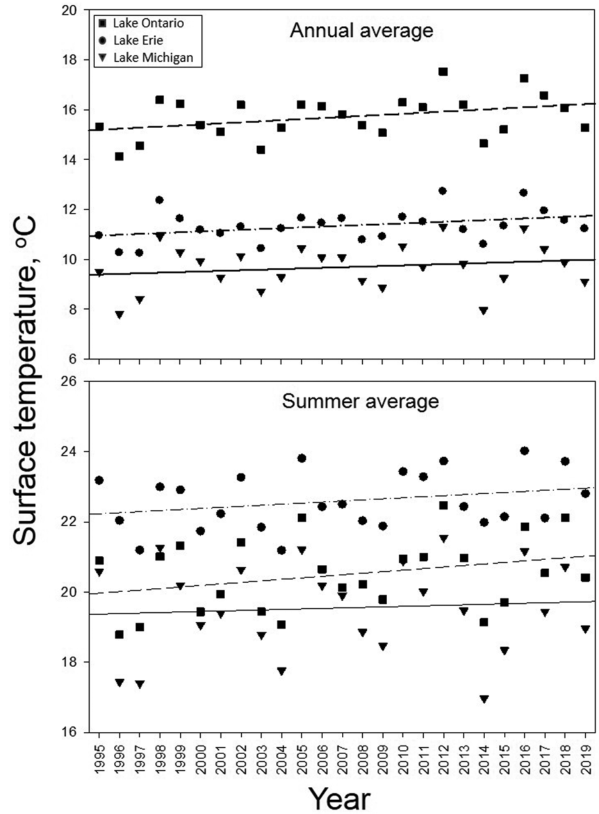

FIGURE 4 Surface water temperatures in lakes Ontario, Erie, and Michigan. Trend lines fitted by least-squares regression (see Section 3) are only marginally significant for annual temperatures in Lake Ontario ($p = 0.066$) and Lake Erie ($p = 0.068$), and insignificant for Lake Michigan. Differences in mean annual and mean summer temperatures between time periods of 1995–2006 and 2007–2019 are not significant ($p > 0.05$) for each of the lakes. *Source*: NOAA Great Lakes Surface Environmental Analysis

comparison tests found no difference between the 2007–2019 and 1994–2006 time periods ($t = -1.746$, $p = 0.094$), although there was a higher number of ship visits during the 1981–1993 compared with 2007–2019 ($t = 2.933$, $p = 0.007$) and 1994–2006 ($t = 2.004$, $p = 0.056$), respectively. An examination of the periods of partial regulation (1995–2006) (1994 data were not available) versus total regulation (2007–2019) showed a significant decline (25.6%) in NOBOB traffic ($t = -4.504$, $p = 0.0002$) in the latter period, whereas ballasted vessels did not differ between periods ($t = 0.348$, $p = 0.731$).

Surface water temperatures for lakes Erie, Ontario, and Michigan showed no precipitous changes between time periods. Positive trends over the span of this study (Figure 4) were marginally significant for lakes Erie (temperature = 0.03 year + 10.92; ${R_{adj}}^2 = 0.101$; $p = 0.068$) and Ontario (temperature = 0.043 year +15.16; ${R_{adj}}^2 = 0.139$; $p = 0.066$), but not for Lake Michigan ($p = 0.350$). Differences in mean annual temperatures between 1995–2006 and 2007–2019 were marginally significant for Lake Erie ($t = -1.489$, $p = 0.075$) and Lake Ontario ($t = -1.559$, $p = 0.066$), but not for Lake Michigan ($t = -0.608$, $p = 0.275$).

4 | DISCUSSION

Given the disproportionate influence of ballast water discharge on recent patterns of invasions in the Great Lakes basin (Mills et al., 1993; Ricciardi, 2006; Ricciardi & MacIsaac, 2000), we contend that vector suppression achieved through ballast water regulation is largely responsible for the substantial and rapid reduction in the rate of discovery of established non-native species after 2006 (Figures 1 and 2). Ballast water exchange was effective in reducing invasions to the Great Lakes because of the massive increase in salinity and reduction of freshwater species in ballast tanks after implementation of the procedure for ships prior to entering the basin (Bradie et al., 2021; Briski et al., 2010); this context is relatively unique, as the majority of the world's ports are situated in marine environments. However, one may hypothesize at least four alternative causes that at first glance could have plausibly contributed to a reduced discovery rate.

4.1 | Alternative hypothesis: Reduced ship traffic

Risk of non-native species establishment increases with propagule pressure—that is, the number of introduction events and number of organisms released per event (Lockwood et al., 2005). Ship traffic is an inexact proxy for propagule pressure, with each de-ballasting ship representing a potential release event (Briski et al., 2012). Therefore, if ship traffic was substantially reduced during the period following 2006, then ballast water regulation might not be the primary cause of the observed decline in invasions. The mean number of visits by all inbound ships to the Great Lakes did not differ significantly between the periods 1994–2006 and 2007–2019 (Figure 3), but the number of NOBOB ships declined by 28.6%. A reduced number of NOBOB ships should have contributed to lower invasion risk; however, this change appears insufficient by itself to account for the massive (87%) reduction in new invasions attributable to ballast water release.

4.2 | Alternative hypothesis: Source pool depletion

The likelihood that a new non-native species will become established in an ecosystem increases with the number of species introduced (Lockwood et al., 2009), which in turn depends on the size of the source species pool connected to the ecosystem via one or more major transportation vectors (Liebhold et al., 2017). Therefore, it could be hypothesized that an attenuation of invasions over time has resulted from depletion of potential invaders in source pools, such that most non-native species that are able to be transported in transoceanic ships have already been introduced to the Great Lakes. On the contrary, dozens of highly invasive species identified as probable future ship-mediated invaders based on their traits, invasion histories, and the environmental suitability of the Great Lakes have not yet established (MacIsaac et al., 2015; Pagnucco et al., 2015; Ricciardi & Rasmussen, 1998; Snyder et al., 2014). Furthermore, any reduction of the pool of potential invaders at donor ports that occurred as species colonize the Great Lakes is at least partly offset by the addition of species spreading to these ports from other non-North American regions (e.g., Nehring & Steinhof, 2015). Source pools in general are expanding worldwide (Seebens et al., 2018) and becoming increasingly integrated with the global port network (Sardain et al., 2019; Seebens et al., 2013). Given the continuous spread of invaders globally, it seems likely that the potential source pool of invaders for the Great Lakes has increased rather than attenuated.

4.3 | Alternative hypothesis: Increased environmental resistance

Invasion risk is limited by characteristics of the receiving environment, including its community composition (biotic resistance) and physical conditions that could be intolerable to poorly adapted organisms (abiotic resistance). Biotic resistance leading to community saturation has rarely been documented in lakes and rivers, and appears to be negligible for large heterogeneous aquatic systems subjected to intensive human activities (Leprieur et al., 2008; Ricciardi, 2001). The long-term rate of discovery of invaders in the Great Lakes between 1835 and the mid-2000s is best described by a concave increasing accumulation curve (Ricciardi, 2006), which is linear after the opening of the St Lawrence Seaway in 1959 (Figure 1) and, contrary to what one would expect if resistance was accruing, shows no indication of saturation prior to the mid-2000s. Abiotic resistance imposed by basin-wide environmental change is also an unsatisfactory explanation for the abrupt decline in invasions after 2007. While climate and water quality variables in the basin have changed measurably over the past few decades (Mahdiyan et al., 2021; Mason et al., 2016), no distinct inflection points mark the postregulation time period. For example, no major thermal shifts in surface water temperatures differentiate the three periods (Figure 4). Current water temperatures are likely well within the thermal tolerances of most freshwater invertebrates and fishes in the major donor region of Eurasia (e.g., Souchon & Tisson, 2012).

4.4 | Alternative hypothesis: Reduced search effort

If a substantial reduction in search effort occurred during the 13-year period after 2006, it might explain the change in discovery rate. However, this explanation is not supported. The Great Lakes National Program Office of the United States Environmental Protection Agency (EPA) samples 12–20 stations in each of the Great Lakes during spring and summer, and has conducted the same annual surveillance programs over the past few decades (personal communication, Dr. Thomas H. Johengen, University of Michigan, Cooperative Institute for Great Lakes Research). This includes the Great Lakes Biology Monitoring Program, which has assessed annual changes in phytoplankton, zooplankton, and benthic macroinvertebrate communities since 1983, and whose objectives include searching for non-native species within these communities (https://www.epa.gov/great-lakes-monitoring/great-lakes-biology-monitoring-program).
For example, zooplankton samples have been collected at 20 fixed stations in Lake Erie since 1998, and this monitoring effort was responsible for detecting two non-native copepods, a non-native rotifer, and a non-native cladoceran in the western basin of the lake between 2015 and 2018 (Connolly et al., 2017, 2018, 2019; Whitmore et al.,

2019). Additionally, over the past 15 years the U.S. Fish and Wildlife Service launched and expanded their aquatic invasive species Early Detection and Monitoring program, which samples the nearshore fish community in the Great Lakes annually at various locations considered to be at high risk of species introductions. Other examples include port surveys for non-native species conducted by the Canadian Aquatic Invasive Species Network in 2011 and 2012 using DNA metabarcoding (Brown et al., 2016), and early detection surveillance for invasive carps in the Great Lakes conducted annually since 2013 by Fisheries and Oceans Canada (e.g., Colm & Marson, 2020). Any confirmed new records of invaders resulting from these monitoring efforts are reported in GLANSIS (NOAA, 2021).

4.5 | Evidence of the effectiveness of saltwater flushing

Further support for the ballast water regulation hypothesis is provided by studies of organisms in residual ballast water and sediment samples from the ballast tanks of ships before and after undergoing ballast treatment. First, total abundance (propagule pressure) of living freshwater and brackish invertebrates (i.e., those deemed most risky) in residual ballast water declined significantly following regulation, from an average of ~2400 to <100 m^{-3} (Bailey et al., 2011). Second, total species richness (colonization pressure) of freshwater invertebrates hatched from resting "eggs" contained in ballast sediments of NOBOB ships declined significantly during the postregulation period, as did the total number of eggs carried in sediment per ship (Briski et al., 2010). Third, colonization pressures of living cladocerans, copepods, and rotifers were reduced from 9 to 3 species, 7 to 1 species, and 19 to 3 species, respectively, in postexchanged ballast water in a BACI-design experiment conducted onboard an operating vessel that began with freshwater ballast. Total propagule pressure of living freshwater invertebrates was reduced by 99.4%–100% in these ballast tanks. This same study revealed almost complete mortality of freshwater benthic invertebrates placed in cages in exchanged but not control (no exchange) tanks. Collectively, these studies demonstrate that both propagule pressure and colonization pressure of freshwater species are reduced in ballast water and sediments following saltwater flushing and exchange.

4.6 | Caveats to interpretation of invasion records

While regulation of the vector responsible for most invasions since 1959 appears to have reduced the vulnerability of the Great Lakes to further invasion, there are some caveats to this conclusion. Recent discoveries of introduced zooplankton, apparently established and in some cases spreading among lakes, suggest that the current risk of invasion from ballast water discharge is not negligible (Connolly et al., 2017, 2018, 2019; Whitmore et al., 2019). These discoveries include the copepod *Thermocyclops crassus* in Lake Erie in 2014 (Connolly et al., 2017), the cladoceran *Diaphanosoma fluviatile* in Lake Erie in 2015 and Lake Michigan in 2018 (Whitmore et al., 2019), the rotifer *Brachionus leydigii* var. *tridentatus* in Lake Erie in 2016 (Connolly et al., 2018), and the copepod *Mesocyclops pehpeiensis* in Lake Erie in 2016 (Connolly et al., 2019). According to these reports, none of the species were observed during long-term monitoring in Lake Erie prior to 2014–2016. *T. crassus* was discovered at low density, and it increased slowly in abundance as well as the number of sites occupied in subsequent years, suggesting a recent invasion (Connolly et al., 2017).

Conversely, it is possible that one or more of these species were present but undetected prior to 2006. Both*T. crassus* and *B. leydigii* var. *tridentatus* were recorded in ballast tank sediments of individual NOBOB ships visiting the Great Lakes in the early 2000s (Bailey, Duggan, et al., 2005; Duggan et al., 2005; Johengen et al., 2005). Also collected from these ships were resting eggs of an unidentified species of *Diaphanosoma* which hatched successfully in the laboratory (Bailey et al., 2004). Time lags between introduction, establishment, detection, and reporting can be on the order of several years for zooplankton taxa that are able to form a sediment bank of resting eggs (Branstrator et al., 2017; Walsh et al., 2016). However, although time lags between introduction and detection exceeding 10 years are conceivable for some species, they are a poor explanation for the unprecedented low invasion rate in 2007–2019, given that detection efforts during that period were at least as high as in the previous periods.

Moreover, it is uncertain whether ballast water release was the vector of introduction for two or more of the aforementioned species. We consider a ballast-water introduction of *T. crassus* to be most probable, although another possibility is human-mediated transport from Lake Champlain, where the species was discovered in 1991 (Connolly et al., 2017). *Diaphonosoma fluviatile*—a Neotropical species whose range includes Texas, Louisiana, and Florida—was initially detected near Toledo, Ohio, which receives transoceanic ship traffic (Whitmore et al., 2019); but a natural northern range expansion through animal-mediated overland dispersal is also plausible (Frisch et al., 2007). The cyclopoid copepod *M. pehpeiensis* has a history of association with ornamental aquatic plants and rice paddy agriculture in various regions of the world, and thus Connolly et al. (2019) considered its occurrence in Lake Erie to be more likely related to the aquatic plant trade or aquaculture than ballast water. Therefore, the vectors of introduction of *D. fluviatile* and *M. pehpeiensis* to the Great Lakes remain unknown and might not be linked to shipping.

4.7 | Ballast water regulation has lowered, but not eliminated, invasion risk

The data suggest that non-ship-mediated invasions have also declined in the Great Lakes between the periods of 1994–2006 (11 species) and 2007–2019 (two species), although the latter period has the same number as was recorded during 1981–1993. Greater awareness of the impacts of invasive species to the Great Lakes economy and ecosystems has driven efforts to control regional sale, transport, and possession of species identified as potential threats, as well as individual behaviors (e.g., bait release, aquarium dumping, overland movement of recreational boats) that contributed to species introductions in the past. Public education, as well as state and provincial regulatory efforts, could have played a role alongside ballast water regulation in reducing the rate of invasion (Morandi et al., 2015; Nathan et al., 2014; Seekamp et al., 2016).

Nevertheless, the Great Lakes remain vulnerable to invasion by species introduced through vectors associated with "live trade"—commerce in living organisms (e.g., ornament pond plants, aquarium pets, bait fish, aquaculture), which is poorly regulated (Howeth et al., 2016; Pagnucco et al., 2015; Rixon et al., 2005). For example, the Tench (*Tinca tinca*), a Eurasian fish and recent invader of the Great Lakes-St. Lawrence River basin, was cultivated in a farm pond and accidentally released into a tributary of the St. Lawrence River in the late 1980s. Its population is expanding in the river around Montreal (Avlijas et al., 2018), and a specimen was captured in eastern Lake Ontario in autumn 2018. Four species of carp (bighead carp, silver carp, grass carp, black carp) cultivated in fish farms in the southern United States and subsequently released in the Mississippi River basin over the past several decades continue to pose a high risk of invading the Great Lakes (Embke et al., 2016; Wittmann et al., 2015). One of these species, grass carp (*Ctenopharyngodon idella*), is reproducing in Lake Erie tributaries and might already be established (Whitledge et al., 2021). There is also the associated risk of introduction of parasites and pathogens during fish stocking activities. A non-native parasitic copepod, *Salmincola californiensis*, was discovered to be prevalent on hatchery-raised Pacific salmonids in Lake Ontario in 2018 and 2019 (Mullin & Reyda, 2020), with an unpublished report of its occurrence in Lake Erie during the 1980s (NOAA, 2021); given the large uncertainty of its introduction date, the species was not included in our analysis. Additionally, in the coming decades climate warming is expected to facilitate invasions by warm-adapted fishes and invertebrates, including species dispersed through live trade (Pagnucco et al., 2015).

We suspect that the Great Lakes remain at risk of ship-mediated invasion by species with attributes facilitating population growth from a very low inoculum released from ballast tanks following open ocean exchange and saltwater flushing. The future addition of ballast water treatment to meet numerically based discharge standards is expected to provide continuing and perhaps enhanced protection (Bradie et al., 2021), although new invasions are still possible since legal discharges of ballast water can include viable organisms up to prescribed performance standard levels (IMO, 2021) and because efficacy of treatment systems in non-saline systems aboard operational ships must be validated. Empirical studies that combined ballast water treatment with ballast water exchange/flushing found reduced risk of freshwater species invasions than either procedure alone (Briski et al., 2015; Paolucci et al., 2015). The latter procedure should be maintained for ships entering the Great Lakes in the future, even if performance standards are imposed on all inbound ships.

To our knowledge, the 2006/2008 regulation is the only case of a policy intervention that is linked to a massive reduction of the invasion rate of a large aquatic ecosystem. Since the current regulations were implemented, the overall rate of discovery of new non-native species declined by 84.6% compared to the partial regulation period. No other equivalent period of time in the documented history of the Great Lakes basin since 1835 has had fewer invaders discovered than the period of 2007–2019, and not since the Second World War has there been as few ballast water invasions ($n = 2$) recorded over a 13-year period (Ricciardi, 2006). If the pre-regulation trend had continued unabated, the expected cumulative number of species since 1959 (extrapolating from Figure 1) would have been 100 ± 6 (99% confidence interval) by 2019, in contrast to the recorded number of 85. While it is impossible to determine with high certainty the full extent to which the 2006/2008 regulation is responsible for this unprecedented decline, multiple lines of empirical evidence discussed above suggest it is the most influential causative factor. The regulation has likely prevented several disruptive invasions, given that at least 30% of non-native species already established in the basin have had demonstrable negative environmental or socioeconomic impacts (NOAA, 2021). This case is an encouraging example of binational response to a transboundary problem, whose apparent success was achieved through rigorous application of an evidence-based, operationally feasible management solution involving participation by governments, the shipping industry, and academia from both countries.

ACKNOWLEDGMENTS

The authors thank three anonymous reviewers for constructive advice, Sunčica Avlijaš and Justin Barker for assistance in the statistical analysis, and Michelle Longworth (St. Lawrence Seaway Management Corporation) for historical data on shipping activities in the Great Lakes. Anthony Ricciardi and Hugh J. MacIsaac gratefully acknowledge funding through the NSERC Canada Discovery Grants program. Hugh J. MacIsaac also acknowledges support from a Canada Research Chair in Aquatic Invasive Species.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Anthony Ricciardi conceived the study and compiled the invasion records, whereas Hugh J. MacIsaac compiled the shipping data. Anthony Ricciardi and Hugh J. MacIsaac both contributed to data analysis and writing the manuscript.

DATA AVAILABILITY STATEMENT

All data used in the figures are taken from published sources described in the text and in Supporting Information.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Ricciardi, A., & MacIsaac, H. J. (2022). Vector control reduces the rate of species invasion in the world's largest freshwater ecosystem. *Conservation Letters*, e12866. https://doi.org/10.1111/conl.12866