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ORIGINAL PAPER

Ballast water management systems protect the Great Lakes from secondary spread of non-indigenous species

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Abstract Approximately 65% of established non-indigenous species (NIS) identified in the Great Lakes–Saint Lawrence River basin (GLSLR) since 1959 were introduced by ballast water discharges from transoceanic vessels. While the rate of new detections has sharply declined, NIS already present may spread within the system—including upstream—through secondary invasions by domestic ballast water transferred mainly by 'laker' vessels. Canada has mandated that all vessels loading or unloading in waters under Canadian jurisdiction in the GLSLR will need to use ballast water management systems (BWMS) by 2030. Here we used simulations informed by empirical data to investigate the expected efficacy of BWMS in reducing zooplankton and phytoplankton introductions on a per-trip basis, and the corresponding probabilities of survival and establishment related to ballast water discharges within the GLSLR. We investigated three ballast water scenarios: no treatment, full treatment, and treatment by a partially-functioning BWMS (owing to malfunctions or challenging water quality). Fully-functioning BWMS reduced community pressure by $>99\%$ and corresponding establishment risk of NIS by 38% and 66% relative to untreated ballast discharges for zooplankton and phytoplankton, respectively. Partial treatment (modelled as a 95% reduction in organism concentrations) resulted in 10–20% reduction in per-trip probability of NIS establishment; results indicate that trips with BWMS inoperability caused by highly turbid uptake conditions may be less risky than trips with BWMS inoperability due to plankton blooms. The implementation of BWMS is expected to reduce risk of secondary spread within the GLSLR system by ballast water, even if the BWMS are subject to periodic malfunction.

Keywords Ballast water management · Ballast water treatment · Great lakes · Invasive species · Non-native species · Non-indigenous species · Secondary spread

Introduction

In the Great Lakes–Saint Lawrence River (GLSLR) region, ballast water has been identified as a pressing environmental threat, having vectored the introduction of zebra (*Dreissena polymorpha)* and quagga

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(*D. rostriformis bugensis*) mussels amongst many others (Ricciardi and MacIsaac 2000, 2022; Allan et al. 2013). A strong link exists between the number of individuals of a species introduced (i.e., propagule pressure) and its establishment risk (Simberloff 2009; Cassey et al. 2018). To reduce invasions, policy makers have focused on reducing propagule pressure in ballast water discharges. For example, voluntary midocean exchange of ballast water by vessels prior to entering the Great Lakes was instituted in 1989 and made mandatory in 1993 (Canada Coast Guard 1989; USCG 1993). This procedure of ballast water exchange (BWE) was later adopted globally by the International Maritime Organization via its Regulation D-1 (IMO 2004). As detections of new species continued in the GLSLR, the focus turned to residual ballast and sediments carried by international vessels (Ricciardi and MacIsaac 2000), leading to mandatory open-ocean flushing to ensure residual ballast water had high salinity. Available data reveal that detections of new introductions of NIS in the GLSLR were sharply curtailed after this procedure was adopted by Canada in 2006 and USA in 2008 (Bailey et al. 2011a; Ricciardi and MacIsaac 2022).

Many invaders—including spiny and fishhook waterfleas (*Bythotrephes longimanus* and *Cercopagis pengoi*), round gobies (*Neogobius melanostomus*), zebra and quagga mussels—spread widely throughout the GLSLR following introduction by international vessels (e.g. Clapp et al. 2001; Benson 2013; Johansson et al. 2018). The majority of ballast water discharges within the GLSLR are made by domestic vessels (i.e., lakers), ~68 million metric tonnes annually (Rup et al. 2010) versus 137,000 to 478,000 metric tonnes by international vessels (EPA 2015). Predictive analyses suggest that ballast water discharges by lakers will rapidly spread invasive species throughout the GLSLR if they are introduced by any pathway (Sieracki et al. 2014; Chenery et al. 2020). Additionally, in the GLSLR, unidirectional downstream flow impedes upstream natural dispersal of most species, but ballast water-mediated transport can bypass this constraint (DFO 2019). Individuals can be transferred in large numbers between source and destination ports within unmanaged laker ballast water, particularly if ballast volume is high and distance travelled short (Briski et al. 2012a). Establishment risk of discharged species would depend on propagule pressure and the degree of environmental matching between source and discharge sites (Chan et al. 2013; MacIsaac et al. 2016). Use of BWE would be ineffective in the GLSLR for various reasons: salinity of source and destination ports are very similar, the lower lakes are not deep enough, and vessels' transit time may be too short to complete BWE.

While vessels that operate only in coastal waters—such as lakers that operate strictly within the GLSLR—never travel to deep ocean areas where BWE is conducted and BWE has been less effective for coastal ports (e.g., Darling et al. 2018; Casas-Monroy et al. 2015), it was recognized that a global replacement for BWE was required (David et al. 2015). The *International Convention for the Control and Management of Ships' Ballast Water and Sediments* established numerical limits on viable organisms in vessels' ballast discharges (Regulation D-2), including: (1) < 10 viable organisms m^{-3} ≥ 50 μm in minimum dimension (hereafter 'zooplankton'); (2) < 10 viable organisms ml^{-1} <50 μm in maximum dimension and ≥ 10 μm in minimum dimension (hereafter 'phytoplankton'); and (3) numerical limits for three indicator microbes related to human health (IMO 2004). The IMO D-2 standards will be fully implemented internationally by September 8, 2024. However, these standards do not apply to vessels that operate only in waters within the jurisdiction of a single country unless that country determines that the discharge of ballast water from such vessels would impair or damage the environment, human health, property, or resources (Article 3.2 of the Convention).

Following research documenting that domestic ballast water movements pose economic and environmental threats (Bailey et al. 2011b; Adebayo et al. 2014; DFO 2019; DFO 2020), Canada extended the IMO D-2 standards to all vessels operating within Canadian waters (Canada Gazette 2021). Canada mandated that lakers constructed since January 1, 2009 must conduct ballast water management using an approved Ballast Water Management System (BWMS) to meet the IMO D-2 standards by September 8, 2024, while vessels built before the era of ballast water management (built prior to January 1, 2009) were given additional time (until September 8, 2030) to overcome unique implementation challenges (Canada Gazette 2021). While the United States has not signed on to the Convention, vessels operating in US waters must meet rules established by the United States Coast

Guard and the Environmental Protection Agency, including discharge standards that are similar to IMO Regulation D-2. Within the Great Lakes, the US standards apply to all international vessels and lakers built after 2008 (2013 VGP2, under the Clean Water Act). To date, at least seven Canadian and two US lakers are equipped with BWMS (S.A. Bailey, unpubl. data).

BWMS reduce the concentration of viable organisms of the entire community, and thus the 'community propagule pressure' in discharged water (Albert et al. 2013).

Ongoing research in the GLSLR suggests that BWMS typically reduce the number of living organisms in ballast water by at least two to three orders of magnitude, even when the IMO D-2 standards are not met (S.A. Bailey, unpubl. data). Previous work estimated that implementation of BWMS by all vessels in the GLSLR would reduce the annual number of species establishments by 83–99%, depending on the proportion of discharges (50–100%) able to achieve the IMO D-2 standard (DFO 2020). Following that pathway-level analysis, this study focuses on risk of individual vessel transits using BWMS within the GLSLR in order to inform decision-making concerning future trip-specific derogation requests when BWMS are malfunctioning or not working. We modeled total organism concentrations of phytoplankton and zooplankton in ballast discharge of lakers, for individual transits where use of BWMS was fully-effective (meets the IMO D-2 standards) and partially effective (treatment is applied to reduce organism concentrations by 95% although the IMO D-2 standards are not met) in comparison to the same trip where no treatment in applied. We then combine these results with estimates of environmental match for origin and destination ports (based on temperature) to predict establishment risk of a given trip within the GLSLR. We also explore how transit-specific characteristics (i.e., high vs. low organism concentration at uptake) may influence risk. We hypothesize that vessel trips with fully operational BWMS will always present lower invasion risks than those with partially-functioning or failed systems even after accounting for environmental dissimilarity of source and destination ports.

Methods

We conducted agent-based simulations using the R programming language (R Core Team 2021) to predict trip-specific species establishment probabilities under three scenarios: (i) no BWMS; (ii) functioning BWMS (discharge compliant with IMO D-2 standards); and (iii) partially-functioning BWMS (hereafter 'partial BWMS') in which a reduction of organisms was achieved even though the discharge fails the IMO D-2 standards. The latter situation may be expected as a result of high suspended solids in the uptake water and/or filter clogging related to presence of gelatinous plankton (Briski et al. 2014). No BWMS refers to when the system has been bypassed (e.g. to avoid malfunctions caused by a high concentration of suspended solids), is inoperable, or not present.

Transit and ballast data were simulated following Bradie et al. (2021). We simulated 1,000,000 voyages, with source port, destination port, and ballast tank volume sampled using empirical transit data from Casas-Monroy et al. (2014). By using empirical data to select port pairs and ballast volumes, we ensured that our analysis used realistic ballast volumes and routes. Uptake concentrations were simulated from theoretical distributions generated by Drake et al. (2020) using empirical zooplankton concentrations in ballast tanks sampled from lakers (Briski et al. 2012a; Adebayo et al. 2014) and phytoplankton concentrations sampled from international vessels arriving to the GLSLR (Briski et al. 2012c), since such data were not available from lakers. Here we consider only zooplankton- and phytoplankton-sized NIS, with no effort to assess risk of IMO D-2 indicator microbes.

A functioning BWMS was assumed to have discharge concentrations < 10 individuals m^{-3} for zooplankton and < 10 individuals ml^{-1} for phytoplankton. Actual concentrations were estimated from levels in successful treatments from field studies, drawn from a Poisson distribution with mean of 1.81 individuals m^{-3} for zooplankton (Bailey et al. 2022) and a Poisson distribution with mean of 1.38 individuals ml^{-1} for phytoplankton (Casas-Monroy and Bailey 2021). Partially-functioning BWMS concentrations were calculated as a 95% reduction to modelled uptake concentrations. Depending on uptake concentrations, this percentage reduction may be sufficient to cause the ballast discharge concentration to become compliant. In this case, concentrations were set to

10 individuals m^{-3} or 10 individuals ml^{-1} for zooplankton and phytoplankton, respectively. Concentrations for vessels with no BWMS were assumed to be unchanged from uptake concentrations.

Environmental match

We used environmental matching based on temperature differences between ballast source and the discharge destination to estimate the initial survival of discharged organisms. Port environmental data were sourced from Keller et al. (2011) and Bradie et al. (2021). We calculated environmental match as the Euclidean distance between standardized temperature variables (mean annual surface water temperature, mean surface water temperature in warmest month, mean surface water temperature in coldest month) for relevant locations (Bradie and Leung 2015).

Following Bradie et al. (2021), we addressed the relationship between environmental match and survival probability using a binomial generalized-linear model fitted with presence-presence distances versus presence-background distances for 603 aquatic species that established in at least one new area. Presence data were obtained for 2014 from the Global Invasive Species Information Network (currently available at https://www.naisn.org/). We generated an environmental distance curve where smaller distance corresponds to a higher environmental match (see Figure S5 in Bradie et al. 2021) and used it to determine if environmental similarity between source and destination ports of each trip would allow organism survival.

Estimating establishment

Surviving species were assessed to determine whether they would establish viable populations based on their initial population size and reproductive capacity. More specifically, species establishment probabilities (1—probability of extinction) were calculated using an adaptation of Leung et al.'s (2004) equation:

$$P_e = 1 - e^{-\alpha N^c}$$

,

where P_e is the probability of establishment, α is a shape coefficient equal to $-ln(1-p)$, p is the probability that a single propagule will establish a viable population, N is the discharge population size, and c is a shape parameter to accommodate an Allee effect (where $c > 1$).

The α parameter is used to capture and quantify species-specific ecological traits that make species more or less likely to successfully establish. Owing to differences in their ecological traits, some species may be able to establish a population even when released at low concentrations, while other species may go extinct even when released at high concentrations. Compliant ballast water discharges may contain dozens of species (Bailey et al. 2022), thus a distribution of α values are required to represent species with different ecological traits and invasion abilities. Previous studies used similar establishment models but, since species-specific traits that determine the likelihood of a species to establish should be based on model assumptions and data sources, there is no accepted standard for α values. Gertzen et al. (2011) estimated p values for aquatic species at 1.5×10^{-2} based on mesocosm experiments with introduced zooplankton species, where a selected number of healthy individuals with appropriate sex ratio were released in a suitable environment. Bradie et al. (2013) estimated p values for aquatic species at 7.0×10^{-4} based on establishment rates for aquarium fishes imported to Canada with propagule loads estimated based on national imports. Suitable α values appear to be model-specific, so it was preferable to model establishment rates based on past establishment data.

We estimated discharge population size, N, by multiplying modelled ballast water concentrations by discharge volume. We assumed no Allee effect ($c = 1$), following Bradie et al. (2013), who showed $c = 1$ to be a reasonable assumption when modelling a heterogeneous group of species in an establishment pathway. We used a Bernoulli trial to determine if each surviving species per trip will establish (1) or go extinct (0). An overview of the model steps and data sources is available in Table S1.1 in Bradie et al. (2022).

Following Bradie et al. (2022), we examined the sensitivity of the model to our α distribution, the magnitude of organism reduction applied, and the method for computing ballast concentrations after partial treatment. Alternative α distribution included two beta distributions with higher per capita establishment probabilities (shape parameters $\alpha = 0.0005$, and $\beta = 5$, and $\alpha = 0.0001$, and $\beta = 5$), and both increased or decreased reductions of 99.5 and 90%, respectively.

Our results compared risk for the ballast water management scenarios using five metrics: (i) the total concentration of individuals discharged at the destination port; (ii) the concentration of non-indigenous individuals discharged at the destination port; (iii) the concentration of non-indigenous individuals expected to survive introduction at the destination port; (iv) the probability of establishment for a single transit; and (v) the mean number of transits until an establishment is expected (i.e. p^{-1}, inverse of the probability of establishment for a single transit). Since some vessels carry ballast water with very high propagule pressure, mean organism concentration can be much higher than the median. For this reason, for i) through iii), we mainly focused on mean concentrations, as each transit was analyzed separately and discharge from one vessel does not influence other vessels. However, we also present median values to provide a picture of concentration on a 'typical' vessel.

Analyses considered results by organism size class and ballast uptake concentration. We classified trips with uptake concentration in the top ten percentile as 'high concentration', while those in the bottom ten percentile were classified as 'low concentration'. We examined risk at these ends of the range because cases where uptake concentrations are very high or very low (the latter in association with high suspended solids; Bilotta and Brazier 2008) are expected to cause BWMS inoperability. Differences in establishment rates between treatments were analyzed using binomial repeated measures mixed models, with post hoc pairwise Tukey contrasts.

Results

Fully-functioning BWMS meeting the IMO D-2 standards for zooplankton and phytoplankton typically reduced community propagule pressure by > 99%, except when the initial concentration was very low (i.e. phytoplankton, low uptake concentration, 90% reduction)(Table 1; Figs. 1 and 2). Partial treatment (modelled as 95% reduction of community propagule pressure) typically

Table 1 Mean total organism concentration upon discharge, mean NIS concentrations upon discharge at the destination port, mean concentrations of NIS (+/− 95% CI) surviving release at the destination port, mean probability of establishment across trips, and mean number of transits until a species establishment is expected (+/− 95% CI)

	Functioning BMWS?	Zooplankton			Phytoplankton		
		All	Low	High	All	Low	High
Mean total concentration upon discharge	No	124,717	368	591,496	169	14	615
	Partial	16,236	21	29,575	13	10	31
	Yes	1.8	1.8	1.8	1.4	1.4	1.4
Mean NIS concentration upon discharge	No	21,989	65	105,044	12	1	44
	Partial	1100	4	5252	0.7	0.1	2.5
	Yes	0.3	0.3	0.3	0.1	0.1	0.1
Mean concentration of NIS surviving release at destination	No	16,043	48	76,411	9	0.7	32
	Partial	802	3	3821	0.5	< 0.1	1.8
	Yes	0.2	0.2	0.2	0.1	0.1	0.1
Probability of NIS establishment per trip	No	1.5E−03	9.2E−04	1.6E−03	2.1E−03	2.4E−03	2.3E−03
	Partial	1.3E−03	7.8E−04	1.5E−03	1.9E−03	2.0E−03	2.1E−03
	Yes	5.1E−04	4.2E−04	5.1E−04	1.3E−03	1.4E−03	1.3E−03
Mean trips until at least one NIS establishment	No	655	1090	611	478	424	427
	Partial	794	1288	681	539	495	472
	Yes	1979	2361	1968	773	694	787

Concentrations are shown in individuals m^{-3} for zooplankton and individuals ml^{-1} for phytoplankton. Ballast water management scenarios include no BWMS, partial BWMS, and fully-functioning BWMS. 'Low' and 'high' indicate voyages where initial uptake concentrations were in the bottom or top 10% observed. 'All' includes low uptake, high uptake and medium uptake

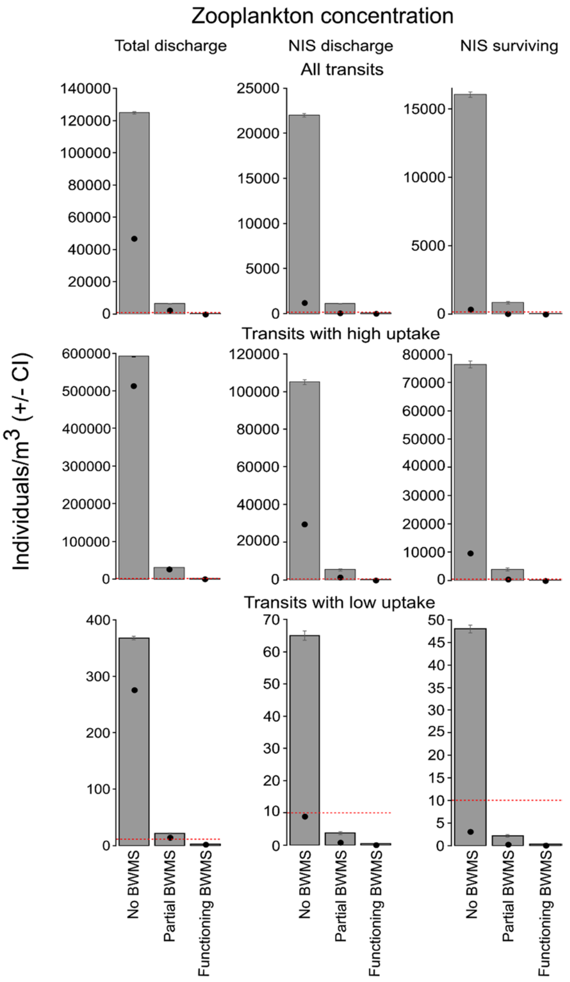

Fig. 1 Mean (bars) and median (black dots) total zooplankton discharge concentration, NIS zooplankton discharge concentration, concentration of zooplankton NIS surviving release at the destination port, and probability that at least one NIS zooplankton establishment will occur with a single voyage. Red dotted line denoted IMO regulation D-2 limit. Values from the y axis are individuals m^{-3} and error bars show +/− 95% CI for the mean. Ballast water management scenarios include no BWMS, partial BWMS, and functioning BWMS. High uptake transits are defined as those where initial uptake concentrations were in the top 10% of concentrations observed. Low uptake transits are defined as those where initial uptake concentrations were in the bottom 10% of concentrations observed. Note scale in the y axis differ from panel to panel, but it illustrates the magnitude of the effect from each BWMS.

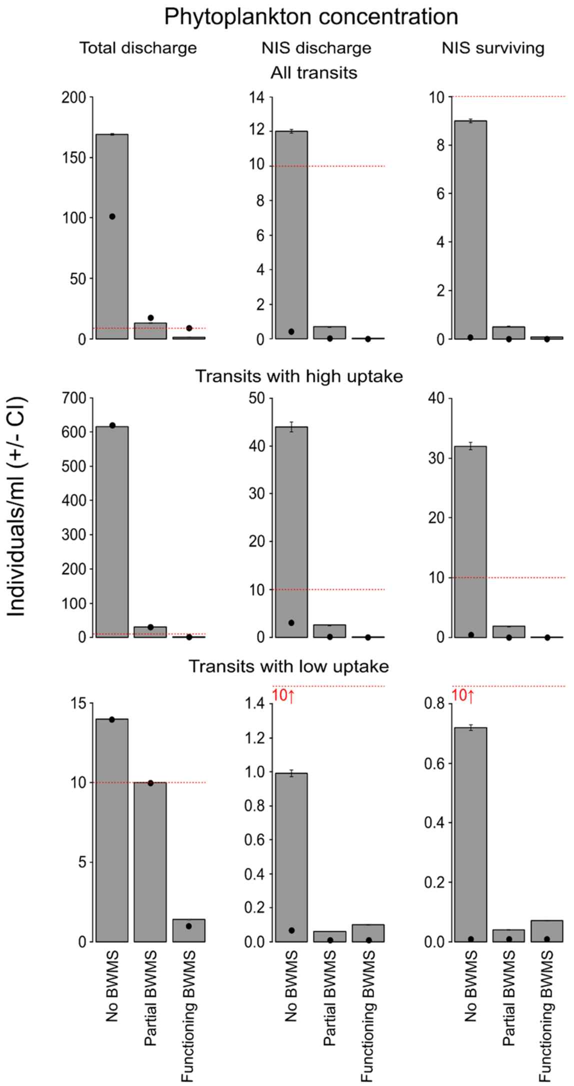

Fig. 2 Total phytoplankton discharge concentration, NIS phytoplankton discharge concentration, concentration of phytoplankton NIS surviving release at the destination port, and probability that at least one NIS phytoplankton establishment will occur with a single voyage. Values from the y axis are individuals ml^{-1}. See Fig. 1 legend for detailed description

resulted in mean zooplankton discharge concentrations of 16,236 individuals m^{-3}, although, when the uptake concentration was low, the IMO D-2 standard was marginally exceeded (21 individuals m^{-3}) (Table 1; Fig. 1). For phytoplankton, partial treatment resulted in mean discharge concentrations near the IMO D-2 standard (31 individuals ml^{-1}), even when uptake concentration was relatively high (Table 1; Fig. 2). When phytoplankton uptake concentration was low, the IMO D-2 standard was frequently met following partial treatment (set to 10 individuals m^{-3} as described in the methods). Lack of treatment resulted in the highest discharge concentrations for zooplankton and phytoplankton, with extreme values being more than four orders of magnitude (i.e., 591,596 individuals m^{-3}) and more than one order of magnitude (615 individuals ml^{-1}) above the IMO D-2 standard, respectively (Table 1; Figs. 1 and 2).

Fully-functioning BWMS dramatically reduced mean concentration of NIS zooplankton in vessels' ballast discharges at the destination port versus untreated vessels (0.3, 21,989 individuals m^{-3}, respectively) (Table 1; Fig. 1). A similar, though less potent, reduction occurred for phytoplankton concentration (0.1, 12 individuals ml^{-1}, respectively) (Table 1; Fig. 2). NIS zooplankton concentration in discharges with partial treatment were also markedly lower than in untreated ballast (1100–5252 individuals m^{-3}), particularly for transits with low concentration at uptake (4 individuals m^{-3}) (Table 1; Fig. 1). NIS phytoplankton concentration in discharges with partial treatment were very low independent of the uptake concentration (<0.1–2.5 individuals ml^{-1}) (Table 1; Fig. 2).

Populations discharged from ballast releases were then subjected to additional reductions depending on the degree of environmental matching between source and destination ports. Environmental match decreased NIS concentrations 27–28% for zooplankton and 27–33% for phytoplankton, with similar effect for treated and untreated ballast water (Table 1; Figs. 1 and 2). The probability of NIS zooplankton establishment was 54–68% lower for fully-functioning BWMS versus untreated water, depending on uptake concentration (Table 1; Fig. 3). The probability of NIS phytoplankton establishment was 38–43% lower for fully-functioning BWMS versus untreated water, depending on uptake concentration (Table 1; Fig. 3). When partial treatment was modelled, the probability of establishment for zooplankton NIS was lowest for transits with low uptake concentrations. The mean number of trips required before a NIS zooplankton species established was inversely proportional to establishment risk. For uptakes with fully-functioning BWMS, the number of trips required until at least one NIS zooplankton becomes established is doubled (from 1090 to 2361) or tripled (from 611 to 1968) when uptake concentrations are low or high, respectively. For NIS phytoplankton, the number of trips was extended 1.6 to 1.8 times, depending on uptake concentration (Table 1). Partial BWMS efficacy resulted in a similar effect on the expected number of trips until at least one NIS establishes, ranging from 1.1 to 1.2 times longer, across all scenarios (Table 1).

Sensitivity analysis revealed that the relative performance of partial BWMS increased as a greater proportion of the species assemblage was eliminated (from 90 to 95 to 99.5%). Until more data are available on the percent reduction achieved by partial treatment, the relative benefit of partial treatment should be treated with caution. Bradie et al. (2022) noted that, for international transits, outcomes of analyses using percentage reduction were similar to those obtained using real data from sampled non-compliant treated ballast water. We expect the same scenario with lakers; however, we could not test it owing to absence of empirical data on treated ballast water from lakers.

For both alternate α distributions examined, we observed a marked decrease in the mean number of transits to establishment. These values (as low as 21 transits to expected establishment) are unrealistic given observed historical reported invasion rate values. Regardless, changing the α distribution did not change the relative performance of the management options.

Discussion

The GLSLR region has the highest number of reported freshwater invasive species in the world (Ricciardi 2006; A. Riccardi, McGill University, unpubl. data). Ballast water release from international vessels accounts for ~65% of introductions since the modern St. Lawrence-Great Lakes Seaway opened in 1959, though there has been a substantial decline in the rate of new detections since 2006 (Ricciardi and MacIsaac 2022). As lakers move ~95% of ballast water within the basin, they appear to be the primary means by which secondary spread of NIS occurs (Rup et al. 2010). Our results indicate that the use of fully-functioning BWMS meeting IMO regulation D-2 standards should reduce phytoplankton and zooplankton discharge concentrations, including concentrations of NIS, by several orders of magnitude. The corresponding per-trip reduction in probability of establishment is reduced by 66% for zooplankton and 38% for phytoplankton. In contrast, the large reduction (95%) in propagule pressure modelled for partially-functioning BWMS only mildly decreased

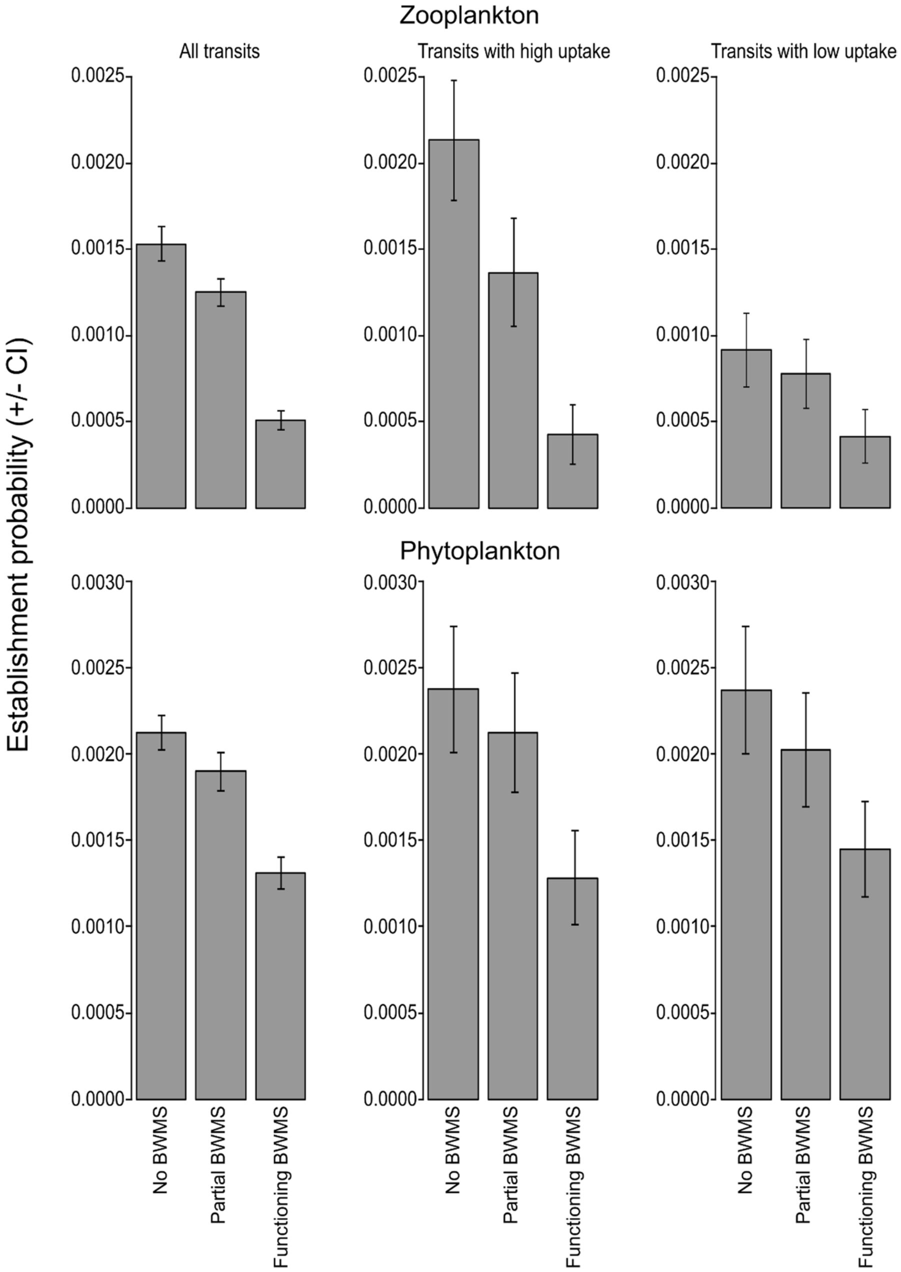

Fig. 3 NIS establishment probability for zooplankton and phytoplankton in three ballast water management scenarios including no BWMS, partial BWMS, and functioning BWMS. High uptake transits are defined as those where initial uptake concentrations were in the top 10% of concentrations observed. Low uptake transits are defined as those where initial uptake concentrations were in the bottom 10% of concentrations observed

per-trip establishment risk (e.g. 13% and 17% for zooplankton and phytoplankton, respectively, versus untreated ballast water). Interestingly, under the partially-functioning BWMS scenario, the reduction in per-trip establishment risk was approximately 2× greater when uptake concentrations were low (rather than high), indicating that trips with BWMS inoperability caused by highly turbid uptake conditions may be less risky than trips with BWMS inoperability due to plankton blooms. Our results also suggest a higher establishment risk for NIS phytoplankton than for NIS zooplankton in all studied scenarios (Table 1).

Environmental match plays an important role in establishment of NIS (Barry et al. 2008; Verna et al. 2018) and is frequently used when estimating invasion risk related to ballast water discharge (e.g. Bradie et al. 2021, 2022). In our study, environmental match reduced NIS survival after discharge by

27–30% across all studied scenarios, thereby reducing both individual species' propagule pressure and community propagule pressure of surviving organisms and, in turn, establishment risk. Bradie et al. (2022) used similar settings in their model and found that environmental dissimilarity reduced propagule pressure by 29 to 35% on international transits indicating that there is a reduced effect of environmental dissimilarity (based on temperature) within the GLSLR.

As the per-trip probability of establishment of NIS is reduced by use of BWMS, the expected number of trips until at least one NIS becomes established will be extended. Previous records of initial introduction and secondary spread in the GLSLR revealed relatively small time-windows between first report of a species in the Great Lakes to their record in all five lakes (i.e. four and five year periods for zebra mussel and round goby, respectively; Poos et al. 2010, Benson 2013). Considering the establishment risk reduction provided by fully-functioning BWMS in our study, we expect that the use of BWMS by lakers will decrease the rate of spread of NIS. A protracted spread interval allows more time to detect and respond to a new invader.

Model assumptions and limitations

Owing to lack of data, we modelled uptake concentrations based on arrival concentrations (spanning a variety of ages, from hours to months old). Available literature indicates that organism concentrations can change following uptake owing to species performance differences while resident in a ballast tank (David et al. 2007; McCollin et al. 2008). Both zooplankton and phytoplankton concentrations tend to decline with holding time in ballast tanks (Gollasch and David 2021), lack of light and/or food (Gollasch et al. 2000), and unfavourable conditions (Olenin et al. 2000). However, some species have been reported to reproduce and increase in population size while in ballast tanks (Bailey et al. 2005; Ardura et al. 2021). Population dynamics inside ballast tanks are likely to be voyage-specific (Gray et al. 2007; Chan et al. 2015) but owing to lack of data that indicated a clear directional change in concentrations between uptake and arrival, we used arrival concentrations as a surrogate for uptake concentrations.

The proportion of NIS species in modelled ballast water was informed by a small number of studies that reported a low number of NIS in comparison with the total plankton community (Briski et al. 2012a; Adebayo et al. 2014; Casas-Monroy et al. 2014). This small NIS species proportion could lead to an underestimate of NIS spread, because of the high number of annual ballast water discharge events and the high number of NIS species in the GLSLR. However, we do not expect this to influence our study as we conducted transit-specific analyses that did not seek to identify which species establish but rather to estimate the number of trips until at least one species becomes established. As we did not set a cap on the number of NIS species per trip, our model allowed the possibility of transits with a high number of NIS. In addition, a lack of data on species-specific α distributions led us to assume the same α distribution for zooplankton and phytoplankton setting α values to 0.005 for all species to assess the effect if all species reproduced clonally—a 'worst case' scenario (Bradie and Bailey 2021). We suggest that future studies investigate species-specific per capita establishment risk that will allow more precise predictions.

In our model, we did not consider ballast sediments as this was beyond the scope of this study. Ballasting operations with no BWMS and inoperable or partially-functioning BWMS, where filters are bypassed, may lead to larger sediment loads and uptake of high concentration of organisms in the tanks. Accumulated sediments may represent a refuge for some organisms that can potentially emerge and be discharged later. Previous studies demonstrated risk associated with ballast sediments as they are a suitable habitat for a range of species and their dormant stages (Bailey et al. 2007; Gray and MacIsaac 2010; Briski et al. 2012b). Organisms found in ballast sediments often have adaptations to hide in or attach to sediments therefore release during ballast water discharge is less likely than for planktonic species (Duggan et al. 2005). In addition, sediments largely remained undisturbed in ballast tanks during de-ballasting events and were only removed during periodic dry-docking (Prange and Pereira 2013). Additional work to understand the efficacy of BWMS for management of ballast sediments is warranted.

Limited data from primarily marine systems reveals very mixed results regarding whether BWMS can achieve IMO D-2 standards (Bailey et al. 2022;

Dong et al. 2023; Xiang et al. 2023). Conceptually, any reduction in community propagule pressure should produce a reduction in invasion risk, though some of the aforementioned studied involved vessels with large exceedances of the IMO D-2 standards. It is essential that more sampling be conducted on vessels operating within the Great Lakes to determine if BWMS operate as designed in strictly freshwater environments.

Conclusions

Modeling exercises informed by empirical data indicate that use of fully-functional BWMS meeting the IMO D-2 standards should result in >99% reduction of zooplankton and phytoplankton discharged with ballast water by lakers in the GLSLR. The use of partially-functioning BWMS significantly reduced community propagule pressure although the probability of NIS establishment was only marginally better than with no treatment (about 10–20% improvement). This was particularly important for transits with high uptake concentrations of organisms where a percent reduction still produced a relatively high propagule load. Conversely, modeled results for partially-functioning BWMS produced approximately 2× greater reduction in per-trip establishment risk when uptake concentrations were low (rather than high), indicating that trips with BWMS inoperability caused by highly turbid uptake conditions may be less risky than those with inoperability associated with to plankton blooms. Use of BWMS on the Great Lakes should reduce secondary invasions of NIS already present in the system, or, at minimum, extend the time interval before such invasions occur.

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Author contributions MRH: writing first draft, graphics, revisions; JBS: conceptualization, modeling; SB: conceptualization, data provision, editing and revisions; MR: conceptualization, writing first draft; HJM: conceptualization, writing first draft, editing, revisions, funding.

Data availability R code for simulations and analysis is available via the Zenodo Digital Repository https://doi.org/10.5281/zenodo.7221898 (Bradie 2022).

Declarations

Conflict of interest The authors declare no competing financial interests.

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