



Richness – abundance relationships for zooplankton in ballast water: temperate versus Arctic comparisons

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Species richness and abundance are two commonly measured parameters used to characterize invasion risk associated with transport vectors, especially those capable of transferring large species assemblages. Understanding the relationship between these two variables can further improve our ability to predict future invasions by identifying conditions where high-risk (i.e. species-rich or high abundance or both) and low-risk (i.e. species-poor and low abundance) introduction events are expected. While ballast water is one of the best characterized transport vectors of aquatic non-indigenous species, very few studies have assessed its magnitude at high latitudes. We assessed the arrival potential of zooplankton via ballast water in the Canadian Arctic by examining species richness, total abundance, and the relationship between the two parameters for zooplankton in ships from Europe destined for the Arctic, in comparison with the same parameters for ships bound for Atlantic Canada and the Great Lakes. In addition, we examined whether species richness and/or total abundance were influenced by temperature change and/or ballast water age for each shipping route. We found that species richness and total abundance for Arctic and Great Lakes ships were significantly lower than those for Atlantic ships. Differences in species richness and total abundance for ships utilizing different shipping routes were mostly related to ballast water age. A significant species richness – total abundance relationship for Arctic and Great Lakes ships suggests that these parameters decreased proportionately as ballast water aged. In contrast, the absence of such a relationship for Atlantic ships suggests that decreases in total abundance were accompanied by little to no reduction in species richness. Collectively, our results indicate that the arrival potential of zooplankton in ballast water of Arctic ships may be lower than or similar to that of Atlantic and Great Lakes ships, respectively.

Keywords: biological invasions, colonization pressure, invasion pathway, invasive species, propagule pressure, shipping vector.

Introduction

The invasion process can be viewed as a series of stages including arrival, survival, establishment and spread, where successful transition to subsequent stages is determined by a number of factors including the number of arriving species and their abundance (i.e. colonization pressure and propagule pressure), physicochemical factors, and community interactions (Kolar and Lodge, 2001; Lockwood *et al.*, 2005; Colautti *et al.*, 2006; Blackburn *et al.*, 2011). Despite the complex nature of the invasion process and the number of factors that influence it, colonization pressure and propagule pressure remain important null models for biological invasions (Colautti *et al.*, 2006; Lockwood *et al.*, 2009). Increasing the number of introduction events or the number of propagules released per event enhances the probability of establishment of a

population due to decreased environmental and demographic stochasticity, respectively (Colautti *et al.*, 2006; Lockwood *et al.*, 2009; Simberloff, 2009). Similarly, a greater number of species introduced increases the potential that at least one species can form a self-sustaining population in the new environment (Lockwood *et al.*, 2009), where matching environmental conditions between source and recipient habitats provides the greatest opportunity for establishment success (Herborg *et al.*, 2007; Barry *et al.*, 2008; Floerl *et al.*, 2013). Therefore, a first step in assessing invasion risk of a transport vector—particularly those capable of transferring large species assemblages—is to determine the arrival potential of transported species by quantifying the number of individuals introduced per species and the number of species released per introduction event (e.g. Conn *et al.*, 2010; Haska *et al.*, 2012; Briski *et al.*, 2013).

Understanding the link between richness and abundance for species assemblages being translocated by a transport vector can further improve our ability to predict invasions by identifying conditions where high- and low-risk introduction events are expected (see Lockwood *et al.*, 2009; Briski *et al.*, 2012). A high-risk introduction event may be characterized by a large number of species each represented by many individuals, a large number of species each represented by few individuals, or by a few abundant species, although we expect the first scenario to represent the greatest invasion risk because of the high likelihood for establishment of multiple species in the new environment. In contrast, a low-risk introduction event may be characterized by a small number of species each represented by few individuals. The relationship between species richness and abundance will depend on the nature of the vector, the source community, and survival and reproductive strategies of entrained organisms (Lockwood *et al.*, 2009; Briski *et al.*, 2012, 2014). For example, Briski *et al.* (2012) reported that the relationship between species richness and total abundance (i.e. total number of individuals of all species) varied across and within taxonomic groups sampled from ballast water of ships.

Temperature change is regarded as a principal environmental factor affecting survival of organisms, including those in ballast water (Gollasch *et al.*, 2000a; Klein *et al.*, 2010; Seiden *et al.*, 2011). Other factors that may also cause mortality in ballast tanks include food limitation, predation, light and oxygen limitation, mechanical injury due to wave action, and chemical toxicity associated with tank coatings (Carlton, 1985; Gollasch *et al.*, 2000b; Wonham *et al.*, 2001). Increasing ballast water age prolongs the interval that organisms are exposed to these stressors, and thus usually adversely affects the number of organisms that survive (Verling *et al.*, 2005; Cordell *et al.*, 2009; Gollasch *et al.*, 2000b). The effects of these selective pressures on organism survival during transport could vary depending on the shipping route because of exposure to different environmental conditions (Briski *et al.*, 2013). As a result, species richness, total abundance, and subsequently the relationship between species richness and total abundance associated with ballast water could vary depending on the shipping route (e.g. Arctic versus temperate voyages).

While ballast water is one of the best characterized vectors of aquatic non-indigenous species (NIS) globally, very few studies have assessed the magnitude of the transport vector in the Arctic (e.g. Niimi, 2004; Chan *et al.*, 2013; Ware *et al.*, 2013), and none have conducted biological sampling to determine community assemblages being transported in northern Canada. Arctic shipping plays an important role in supporting Canada's northern communities by delivering supplies and transporting Arctic resources to domestic and international markets (McCalla, 1994). However, shipping may also provide opportunities for species to disperse into or within the region. For example, the Pacific diatom *Neodenticula seminae* (Simonsen and Kanaya) Akiba and Yanagisawa reappeared in the Labrador Sea in 1999, though it was absent since the Pleistocene (Reid *et al.*, 2007). While evidence suggests that the diatom was likely carried by increased flows of Pacific water from the Bering Sea through the Arctic Ocean following recession of coastal ice sheets, the possibility of introduction via ballast water cannot be dismissed (Reid *et al.*, 2007). At least ten aquatic NIS have been reported in other Arctic and subArctic waters, although the introduction pathway(s) and long-term establishment success are generally not well documented (Hines and Ruiz, 2000; Streftaris *et al.*, 2005; Gollasch, 2006). Such a small number of NIS documented for the Arctic may be an artefact of

limited research effort (Niimi, 2004; Ruiz and Hewitt, 2009). Therefore, an examination of the biological composition of ballast water of ships entering Canadian Arctic waters is needed to evaluate the arrival potential by this vector.

In this study, we determine the arrival potential of zooplankton via ballast water in the Canadian Arctic by comparing species richness, total abundance, and the species richness–total abundance relationship for ships arriving at the Port of Churchill to those bound for ports on the Atlantic coast and in the Great Lakes. Hereafter we use the terms “Arctic”, “Atlantic”, and “Great Lakes” to denote ships destined for Churchill, the Atlantic coast, and Great Lakes, respectively. We have two objectives: first, to quantify species richness and total abundance of zooplankton as well as the relationship between the two parameters in ballast water of Arctic, Atlantic, and Great Lakes ships; and second, to examine transit factors such as temperature change and ballast water age that may influence species richness and total abundance of zooplankton, and subsequently the relationship between the two, in ballast water for different vessel groups. We quantify total abundance of all zooplankton species (i.e. total propagule pressure of all species) rather than abundance per species (i.e. propagule pressure) to be consistent with a number of previous ballast water studies (e.g. Lawrence and Cordell, 2010; Verling *et al.*, 2005; DiBacco *et al.*, 2012) and to be consistent with the D-2 Ballast Water Performance Standard proposed by the International Maritime Organization, which sets a maximum allowable discharge concentration based on the total number of organisms, including zooplankton, per cubic metre of water (IMO, 2004). In addition, because of a major lack of baseline biodiversity information available for Canadian Arctic coastal ecosystems (see Cusson *et al.*, 2007; Archambault *et al.*, 2010), we could not confidently assign invasion status to zooplankton species collected from Arctic ships. The distinction between NIS and native species would also vary depending on the ballast water discharge location (see Briski *et al.*, 2012). As a result, we did not differentiate NIS from native species when determining species richness and total abundance of zooplankton, and thus our results may be conservative estimates of invasion risk for zooplankton in ballast water.

Material and methods

Study sites

The Canadian Arctic covers all Canadian waters north of 60° and also includes Ungava Bay, Hudson Bay, and James Bay (Chan *et al.*, 2012). The Arctic region contains 195 ports, although the Port of Churchill in Manitoba is the only Arctic seaport currently visited by international merchant vessels, which discharge roughly 200 000 m³ of ballast water annually (Chan *et al.*, 2012). There has been no confirmed report of aquatic NIS in the Canadian Arctic, though research effort in the region is low. The Atlantic coast of Canada and waters of the Estuary and Gulf of St Lawrence east of Québec City contain over 77 major commercial ports (Casas-Monroy *et al.*, 2014). The region receives more than 23 000 000 m³ of ballast water released by international merchant vessels each year (Casas-Monroy *et al.*, 2014). At least 112 aquatic NIS have established on the Atlantic Coast of Canada (A. Locke and J. Hanson, unpublished data), though the mechanisms of introduction are not well documented. The Laurentian Great Lakes and the freshwater portion of the St Lawrence River up to and including Québec City contain 15 major ports and 121 regional ports (Bailey *et al.*, 2012). The region receives nearly 5 000 000 m³ of ballast water discharged by international merchant vessels annually

(Bailey *et al.*, 2012). The Great Lakes have been invaded by at least 160 aquatic NIS, with ballast water discharge being a dominant vector since 1959 (Bailey *et al.*, 2012). All international merchant vessels carrying foreign ballast water are required to conduct open ocean ballast water exchange (BWE) prior to entering any of the three regions (Government of Canada, 2006). The BWE procedure replaces ballast water loaded at port with oceanic water, reducing the density of organisms by purging individuals out of tanks and killing remaining ones by osmotic shock (Bailey *et al.*, 2011).

Sample and data collection

We collected zooplankton samples opportunistically from ballast tanks of transatlantic ships arriving at the Port of Churchill between August and October in 2009 and 2010. Using vertical plankton net tows, we collected samples from one tank per ship. We lowered a 30-cm diameter, 30- μm Nitex plankton net through an opened tank access hatch to the maximum accessible depth inside the ballast tank and retrieved it by hand at a speed of $\sim 1 \text{ m s}^{-1}$; this process was repeated until at least 1000 l of water was filtered for analysis. Tow depth ranged from 0.5–4.6 m with a mean depth of 2.1 m (± 0.2 SEM). We preserved all samples in 95% ethanol and stored them at room temperature until analysis. Temperature and salinity of ballast water were measured within the upper 1 m of the water column of each sampled tank using a thermometer and a digital refractometer, respectively. We sorted and enumerated zooplankton in the laboratory using a dissecting microscope, with individuals identified to the lowest taxonomic level feasible with the aid of taxonomic experts (see Acknowledgements). Data on zooplankton richness and abundance in ballast water of transatlantic ships arriving at ports in Atlantic Canada and the Laurentian Great Lakes were obtained from DiBacco *et al.* (2012) and Bailey *et al.* (2011), respectively. Because 125- and 53- μm plankton nets were used, respectively, to collect ballast water samples in the previous studies, we excluded nauplii and rotifers from our analysis to allow for comparison. In addition, many taxa were not identified to species level, and therefore our results should be considered as conservative estimates of species richness. Furthermore, we used data only from ships that took up ballast water at European ports and conducted BWE in the North Atlantic Ocean to reduce the effects of source assemblage on zooplankton species richness and total abundance (Figure 1). The number of zooplankton samples considered in the analysis was 27, 22, and 9 for Arctic, Atlantic, and Great Lakes ships, respectively.

To evaluate the influence of temperature change and ballast water age on species richness and total abundance of zooplankton, we obtained information from Ballast Water Reporting Forms submitted to Transport Canada on the source, volume and age of sampled ballast water, as well as date and location of BWE, for each ship. We used the final coordinates of the BWE event as the start point when calculating temperature change and ballast water age (Figure 1). This was done because environmental conditions and biological composition may change dramatically during the process of BWE (Gollasch *et al.*, 2000b; Gray *et al.*, 2007; Simard *et al.*, 2011). We calculated temperature change as the difference between ocean surface water temperature at the BWE location and that of sampled ballast water. Because measurement of ballast water temperature during BWE was not available, we interpolated ocean surface water temperature at BWE locations in ArcGIS, ESRI Inc. using summer ocean surface water temperature data with a $1^\circ \times 1^\circ$ spatial resolution from the World Ocean Atlas 2009 (Locarnini *et al.*, 2009; Figure 1). We defined ballast water age as the number of days

between BWE and the sampling event. Two Great Lakes ships were excluded from regressions of species richness and total abundance on temperature change because of missing BWE dates, locations, or temperature of sampled ballast water. In addition, one Atlantic ship and one Great Lakes ship were excluded from regressions of richness and total abundance on ballast water age owing to missing BWE dates.

Statistical analysis

Zooplankton richness and total abundance data were log-transformed ($\log [x + 1]$) in all analyses to meet assumptions of parametric tests. We used one-way analysis of variance (ANOVA) and *post hoc* Bonferroni tests to test for differences in species richness and total abundance of zooplankton among vessel groups. The relationship between species richness and total abundance for zooplankton in ballast water for each vessel category was examined using Pearson correlation analysis. To identify factors that might influence species richness and total abundance of zooplankton in ballast water, we tested for differences in range of temperature change and ballast water age among vessel groups using the non-parametric Kruskal–Wallis test because our data did not follow a normal distribution and homogeneity of variances could not be assumed. We conducted follow-up Mann–Whitney tests with Bonferroni correction when a significant Kruskal–Wallis test result was found. Finally, we conducted multiple regression analyses to investigate the simultaneous effects of temperature change and ballast water age on species richness and total abundance of zooplankton in ballast water for each vessel group. In two separate analyses using the forced entry method, species richness or total abundance was entered as the dependent variable, and temperature change and ballast water age were entered as independent variables. The pair-wise correlation matrix, variance inflation factor (VIF), and tolerance statistics were examined to evaluate multicollinearity in models. A significance level of 95% was used for all statistical analyses. All statistical analyses were conducted using SPSS version 21, IBM Corp.

Results

A total of 50 zooplankton taxa were identified from ballast water in transatlantic ships arriving at the Port of Churchill, compared with 62 and 25 taxa for those bound for ports on the Atlantic coast and Great Lakes, respectively (Bailey *et al.*, 2011; DiBacco *et al.*, 2012). Copepods represented the majority of all zooplankton taxa in ballast water of Arctic ships (95% of total zooplankton abundance), followed by gastropod larvae (3%). All other major taxonomic groups, such as amphipods, bivalve larvae, cladocerans, echinoderm larvae, isopods, mites, nematodes, and polychaete larvae, each comprised $<1\%$ of total zooplankton abundance in ballast water of Arctic ships. Similarly, dominant taxa found in ballast water carried by Atlantic ships included copepods (97%), followed by gastropod larvae (1%), with remaining taxonomic groups each consisting of $<1\%$ of the total zooplankton abundance. The zooplankton community in ballast water of Great Lakes ships consisted of mainly copepods (92%), while other taxonomic groups each comprised $<1\%$ of total zooplankton abundance.

There were significant differences in species richness of zooplankton in ballast water of transatlantic ships arriving at Arctic, Atlantic, and Great Lakes ports (ANOVA, $F_{2, 54} = 19.71$, $p < 0.01$). The Bonferroni *post hoc* test revealed that Atlantic ships transported significantly higher zooplankton richness than Arctic and Great Lakes ships ($p < 0.01$ and $p = 0.03$, respectively; Table 1 and

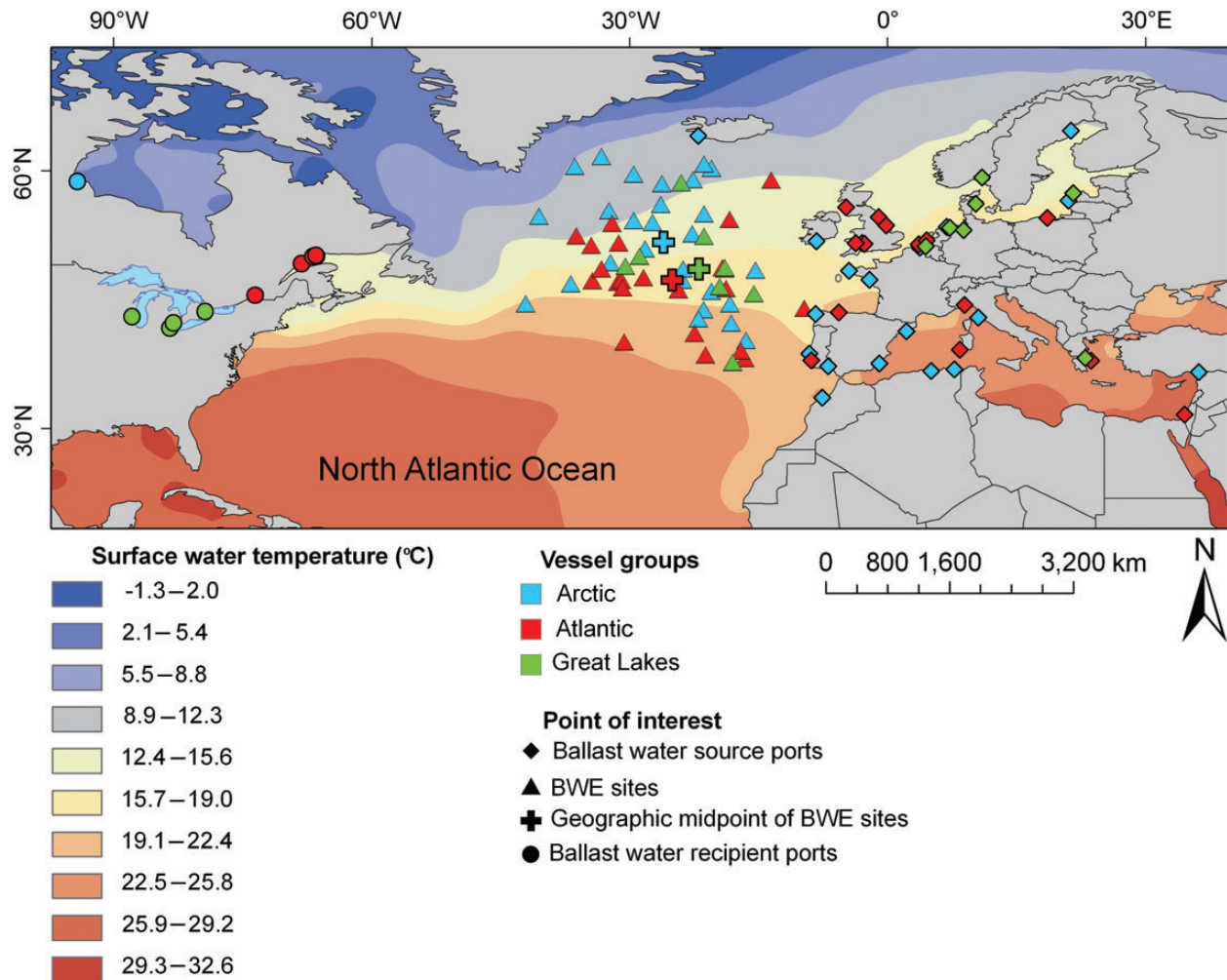


Figure 1. Locations of ballast water source (diamonds), reported final coordinates of ballast water exchange (BWE) sites (triangles), geographic midpoints of BWE sites (crosses), and ballast water recipient ports (circles) for transatlantic ships travelling along Arctic (blue), Atlantic (red) and Great Lakes (green) routes.

Table 1. Summary statistics of species richness and total abundance of zooplankton, range of temperature change, and ballast water age for transatlantic vessels destined for Arctic, Atlantic and Great Lakes ports.

	Arctic	Atlantic	Great Lakes
Species richness (species m ⁻³ of ballast water)			
Range	0–17	6–47	3–15
Mean (±SEM)	4.7 (±0.7)	13.5 (±1.8)*	6.2 (±1.2)
Total abundance (individuals m ⁻³ of ballast water)			
Range	0–9240	213–32823	50–12122
Mean (±SEM)	942.3 (±362.7)	13271.6 (±2381.3)*	2438.6 (±1282.7)
Temperature change (°C)			
Range	0.04–16.4	0.2–12.7	5.3–9.3
Median	6.5	3.8	6.3
Ballast water age (d)			
Range	8–30	3–13	8–17
Median	15.0	7.0*	14.5

Asterisks denote significant difference ($p < 0.05$) from other vessel categories.

Figure 2). However, we found no significant difference in zooplankton richness between Arctic and Great Lakes ships ($p = 0.16$). Similarly, we noted significant differences in total abundance of zooplankton transported by the three vessel categories (ANOVA,

$F_{2, 54} = 23.87, p < 0.01$). The Bonferroni *post hoc* test indicated that Atlantic ships carried significantly greater total abundance of zooplankton than Arctic and Great Lakes ships ($p < 0.01$ in both cases; Table 1 and Figure 2). As with species richness, there was no

significant difference in total abundance between Arctic and Great Lakes ships ($p = 0.50$). We observed a significant positive relationship between species richness and total abundance of zooplankton in ballast water transported by Arctic and Great Lakes ships, though no relationship was found for Atlantic ships (Figure 3).

Our data revealed that there was no significant difference in the range of temperature change for vessels travelling different routes to North America (Kruskal–Wallis, $H_2 = 2.75$, $p = 0.25$; Table 1). However, we found a significant difference in ballast water age among vessel groups (Kruskal–Wallis, $H_2 = 29.6$, $p < 0.01$). A *post hoc* analysis using Mann–Whitney tests with Bonferroni correction showed that Atlantic ships carried significantly younger ballast water than Arctic and Great Lakes ships ($p < 0.01$ in both cases, Table 1), while the latter two groups did not differ ($p = 1.0$).

Multiple regression analyses revealed that temperature change and ballast water age explained a total of 26% and 69% of the variation in species richness of zooplankton for the Arctic ($F_{2, 24} = 4.27$, $p = 0.03$) and Great Lakes ($F_{2, 4} = 4.41$, $p = 0.10$) regions, respectively, but only 9% for Atlantic ships ($F_{2, 18} = 0.88$, $p = 0.43$). Temperature change was not a significant predictor of species richness in any model (Table 2). Ballast water age was a better predictor

in explaining species richness of zooplankton, although it was only significant in the model for ships destined for Great Lakes (Table 2).

A separate multiple regression analysis indicated that temperature change and ballast water age accounted for 47%, 40% and 26% of variation in total abundance of zooplankton transported by Arctic ($F_{2, 24} = 8.55$, $p < 0.01$), Atlantic ($F_{2, 18} = 6.11$, $p = 0.01$), and Great Lakes ($F_{2, 4} = 0.69$, $p = 0.55$) ships, respectively. Total abundance was not affected by temperature in any multiple regression models. Ballast water age was a much more influential predictor for total abundance of zooplankton in Arctic and Atlantic ships (Table 2). We tested for multicollinearity in all multiple regression models by examining the variance inflation factor (VIF) and found that temperature change and ballast water age were weakly correlated (VIFs = 1.85, 1.10, and 1.19 for the Arctic, Atlantic, and Great Lakes models, respectively).

Discussion

This is the first study to examine the biological composition of ballast water discharged in Canadian Arctic waters. We compared species richness, total abundance, and the relationship between these two parameters for zooplankton in ballast water transported by transatlantic ships arriving at ports in the Arctic, Atlantic coast,

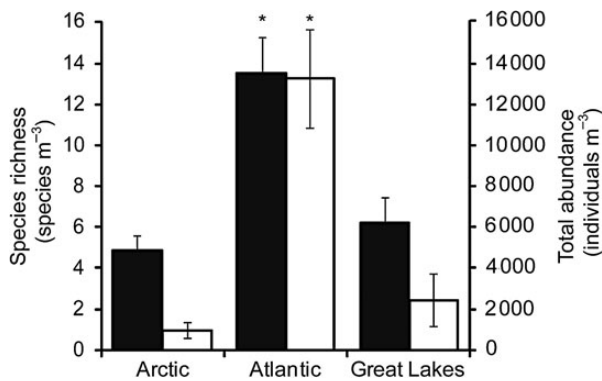


Figure 2. Mean species richness (black bar) and total abundance (white bar) of zooplankton in ballast water transported by transatlantic ships destined for Arctic, Atlantic and Great Lakes ports. Standard errors are included. Asterisks denote significant difference ($p < 0.05$) from other vessel categories.

Table 2. Summary of multiple regression statistics showing simultaneous effects of temperature change and ballast water age on richness and total abundance of zooplankton in ballast water transported by ships arriving at Arctic, Atlantic and Great Lakes ports.

	Arctic		Atlantic		Great Lakes	
	β	p	β	p	β	p
Species richness						
Temperature change ($^{\circ}\text{C}$)	-0.20	0.42	-0.24	0.33	0.26	0.44
Ballast water age (d)	-0.36	0.14	0.26	0.28	-0.90	0.04*
Total abundance						
Temperature change ($^{\circ}\text{C}$)	-0.15	0.47	0.16	0.41	-0.33	0.52
Ballast water age (d)	-0.58	0.01*	-0.66	<0.01*	-0.28	0.59

β denotes the standardized beta coefficient, asterisk indicates significance at 0.05.

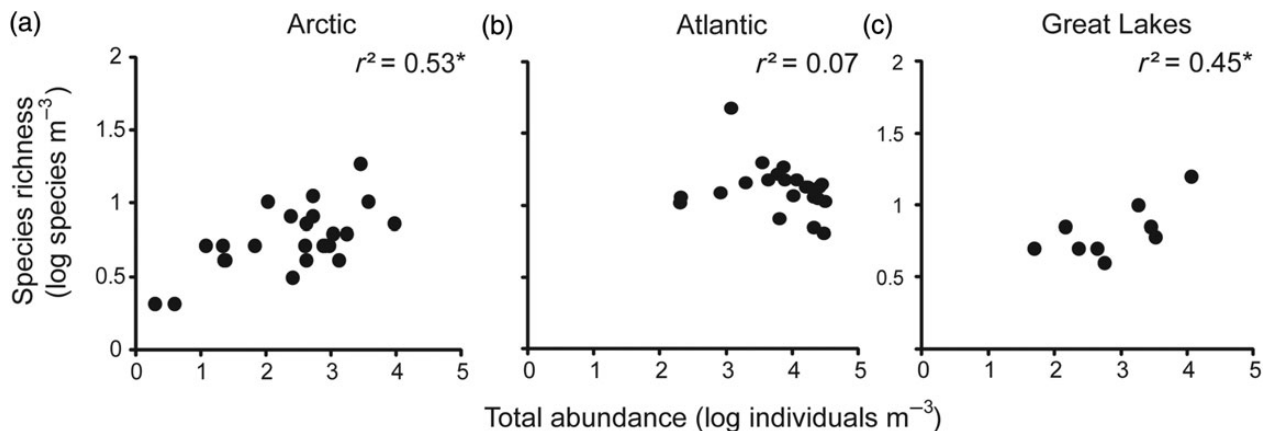


Figure 3. Correlation between richness and total abundance of zooplankton in ballast water collected from transatlantic ships arriving at (a) Arctic, (b) Atlantic, and (c) Great Lakes ports. All data are log-transformed. Asterisks denote significance at 0.05.

and the Great Lakes to determine the relative arrival potential of zooplankton via ballast water in the Canadian Arctic. We found that species richness and total abundance of zooplankton in ballast water transported by Arctic and Great Lakes ships were significantly lower than those for Atlantic ships (Figure 2). Differences in zooplankton species richness and total abundance among vessel groups appeared to be related to ballast water age, with ballast water carried by Arctic and Great Lakes ships being nearly twice as old as that transported by Atlantic ships (Tables 1 and 2). In addition, we detected a significant relationship between species abundance and total abundance of zooplankton for Arctic and Great Lakes ships (Figure 3), indicating that species richness and total abundance decreased proportionately as ballast water age increased. In contrast, the absence of such a relationship for Atlantic ships suggests that decreases in total abundance were accompanied by little to no reduction in species richness. Collectively, assuming higher species richness and total abundance represent a higher likelihood of introduction, and vice versa, our study suggests that arrival potential of zooplankton in ballast water of Arctic ships may be lower than that of Atlantic ships but similar to Great Lakes ships.

The general negative effect of ballast water age on species richness and total abundance of zooplankton was expected. Decreasing species richness and abundance of ballast water organisms with increasing ballast water age have been reported in a number of previous studies (e.g. Gollasch *et al.*, 2000a; Olenin *et al.*, 2000; Verling *et al.*, 2005; Cordell *et al.*, 2009; Briski *et al.*, 2013, 2014). However, the relationship between total abundance and ballast water age was weak for Great Lakes ships. This may be a result of small sample size and limited variation in ballast water age (Table 2). A *post hoc* power analysis conducted using G*Power 3 reveals the statistical power of this analysis was 0.17, indicating a relatively poor ability to detect an effect (i.e. high false negative rate). In addition, our study reveals that ballast water age had a greater short-term effect on total abundance than on species richness of zooplankton. Both species richness and total abundance decreased as ballast water age increased in Arctic and Great Lakes ships that typically had older ballast water (~15 d). In contrast, a decrease in total abundance but not species richness was observed in Atlantic ships (Table 2; Figure 3). In other words, species richness and total abundance decline at different rates with length of entrainment in ballast water tanks, with species richness reducing mainly in older ballast water.

Surprisingly, there were no significant effects of temperature change on species richness and total abundance for any of the vessel groups (Table 2). This may be due to the fact that the transatlantic shipping routes utilized by vessels in this study lie within a relatively narrow latitudinal range (between 30°N and 65°N; Figure 1), where ocean temperature variation is minimal, even for Arctic ships, when compared with other oceanic pathways (Table 1). Taylor *et al.* (2007) noted that the mortality rate of planktonic organisms was significantly higher in ballast water carried by ships that utilize shipping routes spanning temperate to semi-tropical or tropical regions and on transequatorial routes than by those travelling within a narrower latitudinal range. Consequently, we view ballast water age, rather than temperature change, as the principal factor influencing species richness and total abundance of zooplankton, and thus arrival potential of zooplankton via ballast water.

Our results suggest that the arrival potential of zooplankton via ballast water in the Canadian Arctic may be low, and similar to that

in the Great Lakes since implementation of the voluntary and mandatory ballast water management regulations in 1989 and 1993, respectively, which required transoceanic vessels with ballast water to conduct ballast water exchange (BWE) a minimum of 200 nautical miles from the coast in water deeper than 2000 m (USCG, 1993; Transport Canada, 2007). The discovery rate of ballast-mediated NIS in the Great Lakes has declined since the enactment of the ballast water management regulations, with no ballast-mediated invasions reported since 2006 (Bailey *et al.*, 2011). This statistic suggests that managed ballast water released by transoceanic ships poses a low invasion risk for the Great Lakes. BWE is highly effective for the Great Lakes because it replaces coastal organisms entrained at source ports with open-ocean species that are not likely to survive in the freshwater port environment (Gray *et al.*, 2007). The practice may not offer the same degree of protection for the Canadian Arctic because ports there are saline and thereby lack the harmful osmotic effect that kills midocean organisms when discharging into brackish ports. However, Canada's north may be less vulnerable to ballast-mediated invasions for other reasons, in addition to generally low species richness and total abundance of zooplankton in ballast water due to long voyages (Table 1). First, the extent of shipping to most Arctic ports is low relative to temperate and tropical locations, thereby constraining the transfer of species (i.e. few introduction events). In comparison, the Great Lakes receive at least 25 times greater volume of ballast water discharged than the Canadian Arctic each year. Second, environmental mismatch, particularly the low temperature, and limited food resources may hinder survivorship, reproduction, and/or population growth of many species in the Arctic (Vermeij and Roopnarine, 2008; Ruiz and Hewitt, 2009). Temperature differences between BWE locations for Arctic ships and the Port of Churchill ranged from 4.9–16.4°C with a mean temperature of 10.2°C (\pm 0.7 SEM). On the contrary, the invasion risk of ballast water for the Atlantic region is expected to be much higher than for the Arctic and the Great Lakes owing to the relatively high species richness and total abundance of zooplankton in younger ballast water, greater intensity of shipping traffic, and better environmental matching owing to the absence of either a salinity or thermal barrier in this area. However, we were not able to determine the invasion rate of ballast-mediated species in the Atlantic region due to a lack of systematic data.

While the majority of past studies assessed the arrival potential of zooplankton via ballast water based on total abundance of organisms (e.g. Lawrence and Cordell, 2010; Verling *et al.*, 2005; DiBacco *et al.*, 2012), we acknowledge that biological invasions occur at the population rather than the community level. Therefore, we also evaluated the arrival potential of zooplankton via ballast water by comparing mean abundance per zooplankton species (i.e. dividing total abundance of zooplankton by the number of zooplankton species in ballast water) across vessel groups. Our results would not have been affected had we used mean abundance in place of total abundance. For example, mean abundance per species varied significantly among vessel groups (ANOVA, $F_{2,54} = 12.20, p < 0.01$), with Atlantic ships transporting a significantly higher mean abundance per species than other ships (Bonferroni *post hoc* test, $p < 0.01$). The positive relationship between species richness and mean abundance per species was also observed for Arctic (Pearson correlation, $r^2 = 0.23, p = 0.01$) and Great Lakes (Pearson correlation, $r^2 = 0.22, p = 0.20$) ships, though a significant relationship was observed for the former. The opposite pattern was observed for Atlantic ships (Pearson correlation $r^2 = 0.25, p = 0.02$) when mean abundance was considered,

though this pattern was highly influenced by a single datapoint, which, if removed, resulted in a non-significant relationship (Pearson correlation, $r^2 = 0.11$, $p = 0.15$).

We recognize by including only vessels that originated from European ports and performed BWE in the North Atlantic Ocean, the approach reduced, but did not eliminate, the potential effect of source assemblage on species richness and total abundance of zooplankton. Vessels in our study performed BWE over the range from 37–61°N in the North Atlantic Ocean, though the geographic midpoints of BWE locations for the different vessel groups were fairly close by: 51°58'44"N 26°0'10"W, 47°23'10"N 25°3'18"W, and 48°40'14"N 21°51'51"W, for Arctic, Atlantic, and Great Lakes ships, respectively (Figure 1). Continuous Plankton Recorder (CPR) studies have found pronounced spatial variation in zooplankton richness and abundance in the North Atlantic Ocean, including a decrease in species richness with increasing latitude (Colebrook, 1982; Beaugrand *et al.*, 2000, 2001, 2010). In addition, zooplankton communities in the southwestern region of the ocean basin increase in diversity during the summer months, whereas diversity of those in the northern part of the basin remain generally low throughout the year (Figure 5 in Beaugrand *et al.*, 2001). As a result, Arctic ships, which tended to perform BWE at higher latitudes and in colder waters during the summer shipping season, might have collected a less diverse zooplankton assemblage during the BWE process when compared with other vessels. This issue may obscure patterns for Arctic ships.

Although the current arrival potential of zooplankton via ballast water may be low in the Canadian Arctic, it will likely increase in the near future due to warming climate and increased shipping activities. Changes in temperature regimes, ocean currents, and other key physical processes associated with climate change are expected to profoundly influence species dispersal and survival (Hellmann *et al.*, 2008; Vermeij and Roopnarine, 2008; Wassmann *et al.*, 2010; Floerl *et al.*, 2013). For instance, melting sea ice may increase opportunities for ship-mediated introductions in the Arctic by opening new waterways and shipping channels in the Arctic Ocean as well as extending the length of the shipping season (Niimi, 2004; Arctic Council, 2009). Once released in post-warming Arctic waters, species may benefit from enhanced survival associated with warmer climate and increased food supply (Vermeij and Roopnarine, 2008; Cheung *et al.*, 2009). In addition, future development, including increased extraction of mineral and petroleum resources as well as expanded tourism, will further increase exposure of Arctic ports to ship traffic and the potential for species introduction via ballast water discharge (Arctic Council, 2009; Stewart and Howland, 2009).

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