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ARTICLE

Relative importance of vessel hull fouling and ballast water as transport vectors of nonindigenous species to the Canadian Arctic

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Abstract: Ships' hull fouling and ballast water are leading vectors of marine nonindigenous species globally, yet few studies have examined their magnitude in the Arctic. To determine the relative importance of these vectors in Canada's Arctic, we collected hull and ballast water samples from 13 and 32 vessels, respectively, at Churchill, Manitoba. We compared total abundance and richness of invertebrates transported on hulls versus those in ballast water. We found that hull fouling was associated with higher total abundance and richness of nonindigenous species when compared with ballast water. Additionally, a significant positive richness–total abundance relationship for nonindigenous species for hull fouling but not for ballast water assemblages suggests that the likelihood of a high-risk (i.e., species-rich and high abundance) introduction event is greater for the former than the latter vector. The discovery of viable, widespread nonindigenous barnacles in hull samples further underscores the prominence of hull fouling over ballast water as a vector of nonindigenous species. Our study demonstrates that hull fouling is a more important vector for transfer of nonindigenous species to the Canadian Arctic than ballast water based on abundance and richness of nonindigenous species transported by the two vectors.

Résumé : Si les salissures sur les coques de navire et l'eau de ballast sont d'importants vecteurs de transport d'espèces marines non indigènes à l'échelle planétaire, peu d'études ont examiné leur ampleur dans l'Arctique. Afin de déterminer l'importance relative de ces vecteurs dans l'Arctique canadien, nous avons prélevé des échantillons de coque et d'eau de ballast de 13 et 32 navires, respectivement, à Churchill (Manitoba, Canada). Nous avons comparé l'abondance totale et la richesse des invertébrés transportés sur les coques et dans l'eau de ballast. Nous avons constaté que les salissures de coque étaient associées à une abondance totale et une richesse plus grandes d'espèces non indigènes que l'eau de ballast. En outre, une relation positive significative entre la richesse et l'abondance totale des espèces non indigènes dans les salissures de coque, mais non dans les assemblages d'eau de ballast, indiquerait que la probabilité d'un évènement d'introduction de risque élevé (c.-à-d. richesse spécifique et abondance élevées) est plus grande pour le premier vecteur que pour le second. La découverte d'anatifes non indigènes viables répandus dans les échantillons de coque souligne de plus la prédominance des salissures de coque par rapport à l'eau de ballast comme vecteur d'espèces non indigènes. L'étude démontre que les salissures de coque constituent un vecteur plus important pour le transfert d'espèces non indigènes vers l'Arctique canadien que l'eau de ballast, sur la base de l'abondance et de la richesse des espèces non indigènes transportées par les deux vecteurs. [Traduit par la Rédaction]

Introduction

The global shipping network provides an effective dispersal mechanism that allows nonindigenous species (NIS) to bypass biogeographic barriers and reach areas far beyond their natural distributional range (Seebens et al. 2013). Many marine species foul ships' hulls and can dislodge and (or) reproduce at later ports-of-call (e.g., Davidson et al. 2009; Farrapeira et al. 2011; Chapman et al. 2013). Similarly, a wide variety of organisms can be loaded when ballast water is taken on board; thus, its discharge at subsequent ports can release varying numbers of individuals of many different species into the recipient environment (e.g., Cordell et al. 2009; Simard et al. 2011; Briski et al. 2013*a*). At least 237 marine NIS have been introduced worldwide through hull fouling and the discharge of ballast water, resulting in species extinction, alteration of ecosystem function, and economic losses in invaded habitats (Molnar et al. 2008). Given the propensity of vessels to transport NIS, including invasive taxa, much research has been conducted on these vectors to reduce transfers via effective vector management (e.g., Gray et al. 2007; Sylvester et al. 2011; Briski et al. 2013*b*). Very few studies, however, have examined the biological composition of assemblages carried in ballast water of vessels operating in Arctic environments (Hines and Ruiz 2000; Chan et al. 2014), and none have addressed fouling biota transported on vessel hulls. In contrast with the Arctic, hull fouling has received far more attention in the Antarctic and sub-Antarctic (e.g., Lewis et al. 2003, 2006; Lee and Chown 2009).

Although most marine invasions have been reported in tropical to temperate latitudes where the extent of shipping is greatest, the risk of introducing NIS into northern regions via ship vectors (i.e., hull fouling and ballast water) is expected to increase substantially in the near future owing to climate warming and expanded Arctic shipping (Ruiz and Hewitt 2009; Miller and Ruiz 2014). High-latitude waters have experienced a disproportionate increase in sea surface temperature over the past three decades, resulting in melting sea ice and opening of waterways and ship-

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ping channels (Hoegh-Guldberg and Bruno 2010; Smith and Stephenson 2013). For example, the Northern Sea Route between northern Europe and northeast Asia has been traversed regularly by commercial vessels during the summer months since 2009 to save both time and cost of shipping goods (Miller and Ruiz 2014). The Northwest Passage, a similar corridor through the Canadian Arctic Archipelago, was free of pack ice and fully navigable for the first time in recorded history in summer 2007 (Cressey 2007); the first commercial voyage through the passage took place in summer 2013 (Miller and Ruiz 2014). In addition, the volume of shipping traffic in the Arctic has increased rapidly as a result of continued expansion of resource exploration, extraction and export, fisheries, and tourism (Miller and Ruiz 2014). Decline in sea ice extent combined with increased development have also led to lengthening of the shipping season (Pizzolato et al. 2014).

New routes, increased intensity, and a prolonged season will enhance the potential to deliver NIS to high-latitude waters by increasing the abundance and diversity of species (i.e., propagule pressure (PP) and colonization pressure (CP), respectively) transported by vessels. Increasing the number of individuals released per event enhances the likelihood of population establishment owing to reduced demographic constraints, while increasing the number of introduction events enhances establishment probability owing to decreased environmental stochasticity and, possibly, reduced demographic constraints (Simberloff 2009). Likewise, releasing many species increases the likelihood that at least one will form a reproducing population in the new habitat (Lockwood et al. 2009), where matching environmental conditions between donor and recipient sites provides the greatest potential for establishment (Keller et al. 2011; Floerl et al. 2013). Present climatic conditions in certain northern regions are already suitable for temperate species; thus, successful establishment may be possible given sufficient propagule supply (de Rivera et al. 2011). Continued climate warming will further improve the level of environmental match between Arctic and global ports, thereby increasing the vulnerability of high-latitude systems to establishment of introduced NIS (Ware et al. 2014).

In this study, we explore the roles of hull fouling and ballast water as transport vectors of NIS to a major Canadian Arctic port located at Churchill, Manitoba. The objectives of the study are to (*i*) characterize the composition of assemblages transported on hulls and in ballast water of vessels arriving at Churchill and (*ii*) determine the relative importance of these vectors of NIS to the Canadian Arctic by comparing total abundance of all species (total PP), number of observed species (CP), total abundance of all NIS (nonindigenous total PP), and number of observed NIS (nonindigenous CP) transported per vessel. Because ballast water biota discharged into Churchill has been partially characterized in a previous study (Chan et al. 2014), here greater emphasis is placed on investigating those associated with hull fouling. In particular, we examine fouling patterns across various parts of the hull and explore the effects of hull maintenance practices and voyage history on fouling extent on vessels in an Arctic environment. Given limited resources, results of this study can help direct proactive management efforts towards the vector that poses the greater risk such that relatively pristine Arctic ecosystems can be protected from adverse effects of NIS.

Materials and methods

Study site

The Port of Churchill (58°46′59″N, 94°13′0″W) is located on the west coast of Hudson Bay, a large inland sea connected to the Arctic Ocean via the Foxe Basin in the north and the Labrador Sea (via Hudson Strait) in the east (Fig. 1). Mean annual water temperature at Churchill is 4.3 °C (mean range 2.5–8.1 °C), with annual salinity averaging 26.3 ppt (Boyer et al. 2005). Churchill's primary shipping activity is the export of grain owing to its proximity to the Canadian prairies and shorter route to ports in Europe and Africa as compared to alternatives (e.g., Port of Thunder Bay; Niimi 2007). Future expansion in shipping is expected as plans exist to increase and diversify commodities imported and exported through the Arctic Bridge Gateway — a seasonal trade route linking Churchill to the Port of Murmansk, Russia (Gavrilchuk and Lesage 2014). To date, there have been no ship-mediated NIS reported in the Canadian Arctic, including Churchill, but systematic surveys to detect NIS have been limited (Goldsmit et al. 2014). Thus, absence of evidence should not be mistaken for evidence of absence.

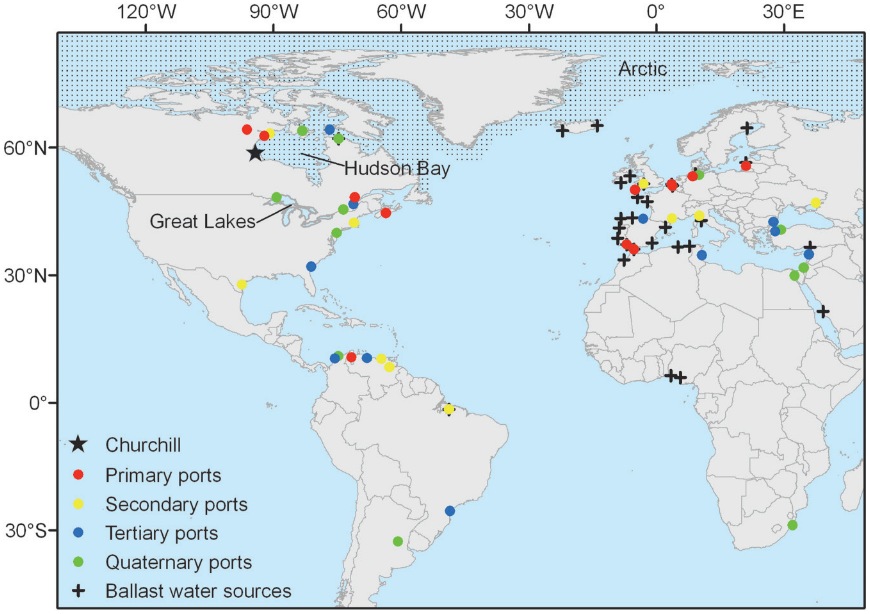
Churchill is the port at greatest risk of NIS introductions via ship vectors in the Canadian Arctic because it receives the largest number of vessel arrivals (about 18 international merchant vessels per year) and volume of ballast water discharge (roughly 200 000 m^3 per year); in addition, its environmental conditions broadly match those of global ports that contain high-impact NIS with which it is connected (Chan et al. 2013). Examples of these ports include Amsterdam, Netherlands, and Hamburg, Germany, where a suite of well-recognized NIS including *Cercopagis pengoi* (fishhook waterflea), *Dreissena polymorpha* (zebra mussel), and *Styela clava* (stalked sea squirt) have been recorded (Chan et al. 2013). In comparison, other major ports in the Canadian Arctic, such as Iqaluit, Nunavut, and Deception Bay, Quebec, receive far fewer vessel visits (9 to 12 arrivals) and less ballast water discharge (4000 to 8000 m^3) annually (Chan et al. 2012, 2013). Furthermore, these ports are primarily connected to domestic ports that contain relatively few high-impact NIS (Chan et al. 2013). Therefore, measurements of total PP and CP associated with hull fouling and ballast water made at Churchill can be considered as the highest risk benchmark for the Canadian Arctic.

Hull fouling survey

We surveyed hulls of 13 vessels visiting Churchill from August to September of 2010 and 2011. These vessels included nine bulk carriers, two general cargo ships, one roll-on roll-off vessel, and one supply tug. Sampling was opportunistic, based on availability of ships and tidal currents. We collected and processed hull samples and underwater footage following the procedures outlined in Sylvester and MacIsaac (2010). Briefly, divers surveyed and recorded video of the full length of each vessel's main hull and niche areas, including topographically complex locations such as bulbous bow and stem, sea-chest grating, stern tube, rope guard, propeller nose cone and blades, as well as rudder side, bottom, leading, and trailing edges. Divers were not able to inspect the sea-chest grating of six vessels for safety reasons. To ensure all underwater locations were surveyed effectively, we collected biological samples from vessels using a stratified sampling strategy in which divers haphazardly collected zero (if lacking fouling) to three replicate quadrats (20 cm × 20 cm each) of fouling biota from each location. Divers collected fouling samples using a scraper and resealable plastic bags or a sampling syringe with a mounted blade. Because each sample often included a volume of port water surrounding the ship, divers also collected three water samples of about 1 L each at depths corresponding to the waterline, mid-hull, and keel of vessels to be used as controls (see below). We immediately examined all samples in sorting trays at the surface to determine whether organisms were alive or dead when collected; this analysis was limited to organisms such as amphipods, bivalves, and cirripedes that were large enough to be checked reliably with the naked eye. We sieved hull and port water samples through a 45 μm mesh and preserved them in 95% ethanol at room temperature until analysis. We obtained ship particulars and plans, including date of last dry-docking and antifouling paint application, and the last 10 ports-of-call from vessels' personnel.

We processed and enumerated hull samples in the laboratory using a dissecting microscope, with individuals identified to major taxonomic groups. We collected a minimum of 30 individuals

Fig. 1. Map illustrating ports-of-call visited by vessels during the last four voyages preceding hull fouling surveys in Churchill. Primary ports (red circles) are origins of non-stop voyages to Churchill. Secondary (yellow circles), tertiary (blue circles), and quaternary (green circles) ports are those visited by vessels one, two, and three voyages before the ultimate voyage to Churchill, respectively. Note data from past 10 voyages were used in analyses, but only last four ports-of-call are presented for brevity. Sources of sampled ballast water (black crosses) are also shown. The Arctic region (dot hatch pattern) is defined following the Arctic Register of Marine Species (Sirenko et al. 2014).



per morphotype and identified them to the lowest taxonomic level feasible with the aid of taxonomic experts (Sylvester and MacIsaac 2010; see Acknowledgements). We were not able to identify many individuals to the species level; thus, our analysis may underestimate the true species richness of transported assemblages (the same applies to ballast water samples; see below). In all samples, algal cover was limited to relatively thin films lacking reproductive structures; therefore, we focused our efforts on invertebrates. We classified taxa into five categories based on their known occurrences: (1) Hudson Bay: taxa that have previously been reported in Hudson Bay; (2) Canadian Arctic: those that are absent from Hudson Bay but have been recorded elsewhere in the Canadian Arctic, including all waters north of 60° and those in Hudson Bay, James Bay (Baie James), and Ungava Bay (Baie d'Ungava) (Canadian Coast Guard 2014); (3) Arctic: those that have not been found in Canada but are known elsewhere in the Arctic, which is defined as "areas within the seasonally averaged 2 °C surface isotherm or the median maximum sea-ice extent, whichever is greater" (Fig. 1; Sirenko et al. 2014); (4) non-Arctic: taxa whose distributions include only areas outside of the Arctic; and (5) unknown: taxa whose distribution could not be determined because they were not identified to species level. For the purpose of the study, we considered Hudson Bay species to be native to Churchill, and treated Arctic and non-Arctic species as NIS. We classified Canadian Arctic species as cryptogenic because their invasion status could not be determined with confidence owing to insufficient baseline biodiversity information for Canada's Arctic coastal systems (see Goldsmit et al. 2014). We determined taxa distributions based on an extensive literature review of scientific journal publications, taxonomic keys, government reports, and online biodiversity databases, as well as consultation with taxonomic experts (see Appendix A, Tables A1 and A2, and Acknowledgements). In addition, we evaluated the potential survival for NIS if released into Churchill based on thermal and salinity tolerances documented in the literature (see Appendix A, Tables A1 and A2).

We excluded species present in control water samples from abundance and richness estimates, assuming they originated from the port community and are not hull fouling organisms. Alternatively, we could correct abundance and richness counts by subtracting individuals in hull samples from those in the equivalent volume of water samples (see Sylvester and MacIsaac 2010). Both approaches provided qualitatively similar results; therefore, we reported estimates calculated using the first method to err on the conservative side. To estimate total PP (or nonindigenous total PP) for the entire vessel, we combined abundance data with percent cover information obtained from video footage, following Sylvester and MacIsaac (2010). We obtained 30 still images from 1 to 1.5 h of footage per vessel using a random stratified design, in which videos were randomly paused and two to five pictures were taken at each location. We superimposed a 100-point grid over each image to estimate percent cover and then averaged the percent estimates to obtain an overall value for each location. We also calculated the surface area of each underwater location by approximating each to simple geometric forms using technical information from ship particulars and plans (see Sylvester and MacIsaac 2010). We estimated abundances per location by multiplying mean abundances in hull samples by the location's percent cover and surface area, then dividing by the surface area of the sampling quadrat (0.04 m^2). Finally, we obtained total PP per vessel as the sum of abundances in all locations.

Ballast water sampling

We opportunistically sampled ballast water of 32 vessels, including 28 bulk carriers and four general cargo ships, arriving at Churchill between August and October of 2009 and 2010. We surveyed four of these vessels, all bulk carriers, simultaneously for hull fouling in 2010. We collected invertebrate samples from one tank per ship before ballast water was discharged. In addition, we collected five baseline harbour water samples, roughly 1000 L each, using plankton net tows (30 cm diameter, 30 μm mesh). Methods for sample collection, enumeration, and taxonomic identification are detailed in Chan et al. (2014). We assumed preserved organisms were alive at the time of collection if they appeared to be in good condition when examined in the laboratory.

We grouped identified taxa into five categories using the same criteria as described previously. We considered taxa present in port water samples to be native to Hudson Bay.

To estimate total PP (or nonindigenous total PP) in ballast water per vessel, we multiplied abundances observed in samples by the volumes subsequently discharged into Churchill. In four cases, the proposed discharge volume included ballast water from two different neighbouring source ports within a short period of time (<5 days). We assumed that collected samples were representative of ballast water from both sources because all ballast was exchanged in the North Atlantic Ocean prior to arrival in Churchill.

Statistical analyses

To evaluate whether sampling effort was adequate in characterizing the true species richness in hull fouling and ballast water assemblages, we estimated asymptotic species richness for each ship sampled using Chao-2 and Chao-1 species richness estimators, respectively. The Chao-2 richness estimator is recommended for replicated incidence or abundance data collected over a heterogeneous habitat, such as the hull fouling survey in this study, whereas Chao-1 is suitable for abundance data collected from a single representative sample from a community, as was the case with ballast water sampling (Gotelli and Colwell 2011). We obtained Chao-1 and Chao-2 species richness estimates using EstimateS version 9.1.0 (Colwell 2013).

We used independent *t* tests to explore differences in total PP and CP for invertebrates transported on vessels' hulls versus those in ballast water, assuming that the two vectors operated independently (see Hewitt et al. 2009). We $\log(x + 1)$-transformed all variables to meet assumptions of parametric tests. We performed separate *t* tests for four vessels from which both hull and ballast water samples were collected for a direct comparison of the vectors for the same vessels. We conducted similar analyses to compare the same variables between vectors using data from all sampled vessels ($n = 45$). In addition, we compared nonindigenous total PP and nonindigenous CP between the two vectors using the nonparametric Mann–Whitney *U* tests because the data did not follow a normal distribution. Again, we performed separate analyses for comparisons within ($n = 4$) and across ($n = 45$) ships. Furthermore, we examined the relationship between CP and total PP and between nonindigenous CP and nonindigenous total PP for hull fouling and ballast water assemblages using Pearson and Spearman's correlation analyses, respectively. We excluded vessels carrying no organisms from analyses because no relationship is expected when inoculum size is small (Lockwood et al. 2009; Briski et al. 2012). We conducted analyses using observed (i.e., CP and nonindigenous CP) and estimated (i.e., Chao-1 and Chao-2) richness and obtained qualitatively similar results; thus, only those obtained using the former are presented to be consistent with previous studies (e.g., Briski et al. 2012; Chan et al. 2014).

To examine fouling patterns on vessels, we tested differences in percent cover across underwater locations on the hull using the Kruskal–Wallis test. We also assessed differences in fouling coverage between the main hull and niche areas of vessels using the Wilcoxon signed-rank test. We used nonparametric tests because data did not conform to a normal distribution and homogeneity of variances could not be assumed. In addition, we compared species richness among all locations using Chao-2 richness estimate, where nonoverlapping 95% confidence intervals denote significant differences. We generated sample-based rarefaction curves to standardize richness across locations on the basis of a common number of samples (Gotelli and Colwell 2011).

We conducted a series of simple linear regression analyses to test the effects of hull maintenance practices and voyage history on fouling extent on vessels. We included percent cover (separately for overall, main hull, and niche area fouling), total PP, CP, and Chao-2 richness estimates as response variables, whereas predictor variables were represented by age of antifouling paint, total port residence time (in the last 10 ports-of-call), and number of bioregions visited (during the last 10 voyages). We grouped ports into nine bioregions following the Marine Ecoregions of the World (Spalding et al. 2007), which included the Arctic, Central Indo-Pacific, Temperate North Atlantic, Temperate North Pacific, Temperate South Africa, Temperate South America, Tropical Atlantic, and Western Indo-Pacific, as well as the Laurentian Great Lakes (Fig. 1). While sailing speed can be a key determinant of fouling extent (Davidson et al. 2009; Sylvester et al. 2011), we excluded speed from analysis because of the relatively low values (~10 knots; 1 knot = 1.852 km·h^{-1}) and minimal variability among vessels. We visually inspected model residuals to check for linearity of the relationship between dependent and independent variables, homoscedasticity of the errors, and normality of the error distributions. We used a significance level of 95% for all statistical analyses. We conducted all statistical analyses using SPSS version 22 unless otherwise stated.

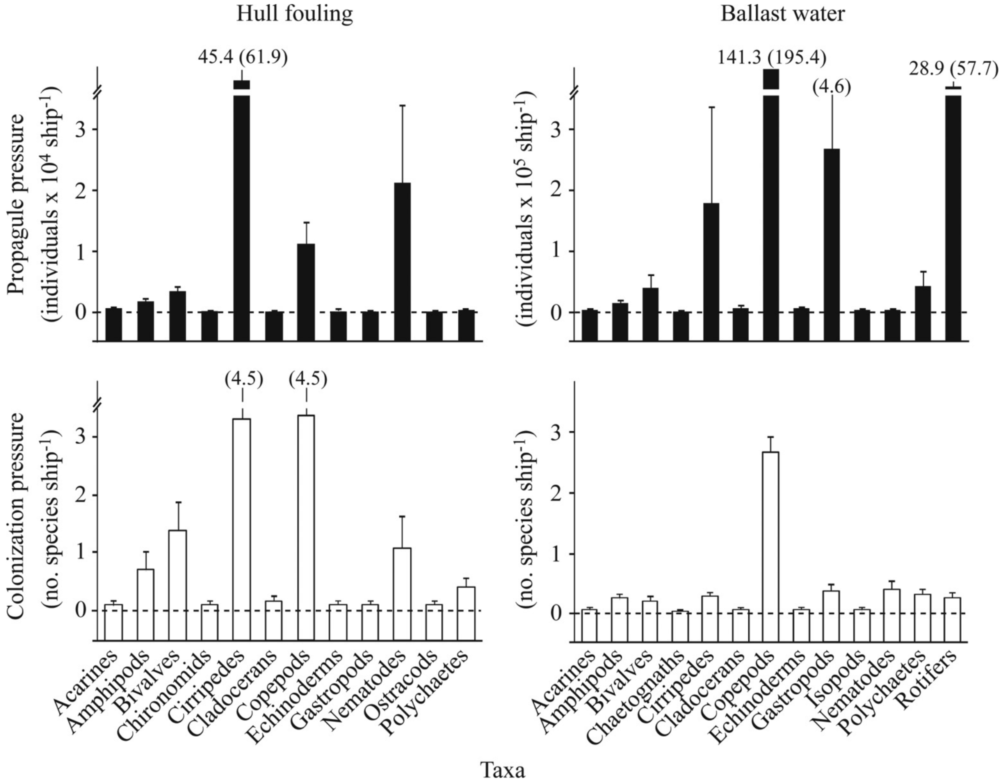
Results

Vessels surveyed for hull fouling visited both foreign and domestic ports prior to arrival at the Port of Churchill (Fig. 1). Typical sailing speed of vessels ranged from 7.0 to 11.2 knots (mean 9.9 knots). Wetted surface area ranged between 496 and 6782 m^2 (mean 5428 m^2). Time since last dry-dock and antifouling paint application varied between 129 and 698 days (mean 392 days). Percent fouled surface area was variable, ranging from 0.0% to 28.1% (mean 4.3%). Total PP in hull fouling assemblages varied from 0.0 to 3.3×10^6 individuals per vessel, with a mean of 4.9×10^5 individuals. Chao-2 richness estimate averaged 29.4 species per vessel, with a maximum of 79.4, and was 2.7 times higher than the mean observed CP (11.0 species).

We identified 86 distinct invertebrate taxa from hull samples, excluding taxa found in port water (Appendix Table A1). Cirripedes represented the majority of all fouling taxa (92% of total PP per vessel), followed by nematodes (4%) and copepods (2%) (Fig. 2). Cirripedes and copepods were also the most species-rich taxonomic groups, followed by nematodes (Fig. 2). There were 15 non-Arctic taxa, including 11 cirripede, one cladoceran, two copepod, and one nematode taxa (Appendix Table A1). Seven of these species are well-recognized hull fouling NIS that have established elsewhere in the world, including *Amphibalanus amphitrite*, *Amphibalanus eburneus*, *Amphibalanus improvisus*, *Amphibalanus reticulatus*, *Austrominius modestus*, *Balanus trigonus*, and *Megabalanus coccopoma*. These nonindigenous barnacles occurred mostly (86% of the time) in samples collected from niche areas of vessels. Live specimens were found for the first six species, which accounted for 0.3%, 25%, 93%, 17%, 100%, and 100%, respectively, of total abundance of each of these species. However, only *Amphibalanus amphitrite*, *Amphibalanus eburneus*, *Amphibalanus improvises*, and *Austrominius modestus* have the potential to survive if propagules are released into Churchill based on their known temperature and salinity requirements. Tolerance information was not available for two copepods, *Paronychocamptus huntsman* and *Schizopera clandestine*, and one nematode, *Prochromadora orleji*. These species are commonly found in cold temperate, coastal waters and thus may have the ability to tolerate environmental conditions in Churchill. With the exception of *Megabalanus coccopoma*, *Megabalanus* cf. *spinosus*, and *Megabalanus* cf. *tintinnabulum*, for which only empty shells were found, as well as the freshwater cladoceran *Acantholeberis curvirostris*, all remaining non-Arctic taxa could potentially survive if released into the port environment. Furthermore, we found two Arctic amphipod species, *Crassicorophium bonellii* and *Jassa marmorata*, and one nematode taxon, *Geomonhystera* sp., which have not yet been reported in the Canadian Arctic and potentially could also survive in Churchill.

Between 5696 and 26 718 m^3 of ballast water per vessel (mean 10 456 m^3) was discharged at Churchill during the sampling period. The majority of this water originated from foreign ports in the

Fig. 2. Mean propagule pressure (solid bars) and colonization pressure (open bars) of invertebrate taxa estimated in hull fouling (left panels) and ballast water (right panels) assemblages transported per vessel. Values off the scale are indicated. Standard errors are also included, in parentheses when off scale. Note the differences in scale and taxa among plots.



Temperate North Atlantic and was exchanged in the North Atlantic Ocean, except for one case in which it was taken from another Canadian Arctic port (Deception Bay – Baie Deception) and was not exchanged (Fig. 1). Total PP in ballast water varied from 0.0 to 1.6×10^8 individuals per vessel, with a mean of 1.7×10^7 individuals. Chao-1 richness estimate averaged 5.3 species per vessel, with a maximum of 20.0, and was very similar to observed CP (mean 5.1 species).

Invertebrates in ballast water samples belonged to 58 distinct taxa (Appendix Table A2). Copepods (80%), rotifers (16%), and gastropods (2%) comprised the largest contributions to total PP per vessel (Fig. 2). Copepods also represented the most diverse taxonomic group, followed by nematodes and gastropods (Fig. 2). We found two non-Arctic species, a copepod, *Nitokra lacustris*, and a nematode, *Daptonema tenuispiculum*; however, they are not likely to survive the cold temperatures in Churchill. We observed five Arctic taxa (two copepod species, *Centropages typicus* and *Heterolaophonte strömi*, and three nematode taxa, *Ascolaimus* sp., Axonolaimidae, and *Geomonhystera* sp.) that could tolerate environmental conditions in Churchill.

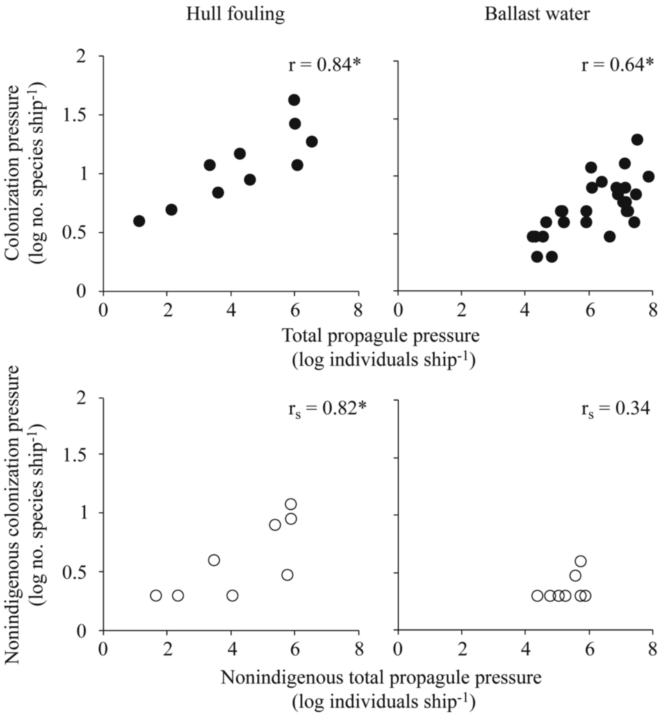
When considering only the four vessels from which both hull and ballast water samples were collected, total PP was significantly lower for hull fouling than for ballast water ($t_6 = -2.94$, $p = 0.03$), while CP did not differ between the two vectors ($t_6 = 0.32$, $p = 0.76$). There were no differences in nonindigenous total PP and nonindigenous CP between vectors within the same vessels ($U_8 = 2.0$, $p = 0.11$ in both cases). When all vessels were considered, total PP again was significantly lower for hull fouling than for ballast water ($t_{43} = -4.37$, $p < 0.05$), whereas CP did not differ between vectors ($t_{43} = 0.96$, $p = 0.34$). In contrast, both nonindigenous total PP and nonindigenous CP were significantly higher across hulls than across ballast water of vessels ($U_{45} = 139.0$, $p = 0.04$ and $U_{45} = 117.0$, $p < 0.01$, respectively), suggesting a greater potential introduction risk for the former vector. We found a significant positive relationship between CP and total PP as well as between nonindigenous CP and nonindigenous total PP for hull fouling assemblages (Fig. 3). Similarly, CP was positively correlated with total PP for ballast water assemblages; however, such a relationship was not observed when considering only NIS (Fig. 3).

Percent fouled area varied significantly across different underwater vessel locations ($H_8 = 15.19$, $p < 0.05$) but not between the main hull and all niche areas together ($Z_{13} = -1.37$, $p = 0.17$). Propellers and sea-chest gratings were typically most heavily fouled relative to other locations (Fig. 4*a*). However, Chao-2 richness estimates did not vary significantly by location (Fig. 4*b*); sample-based rarefaction curves confirmed this was not due to differences in sample size across locations (not shown). Age of antifouling paint was positively related to fouling coverage on the entire vessel and on the main hull, but not in niche areas (Fig. 5). Neither total port residence time nor number of bioregions visited was a significant predictor of percent cover of fouling on ships ($p > 0.05$ in all cases). None of the other variables examined — including total PP, CP, or Chao-2 richness estimates — were influenced by age of antifouling paint, total port residence time, or number of bioregions visited ($p > 0.05$ in all cases).

Discussion

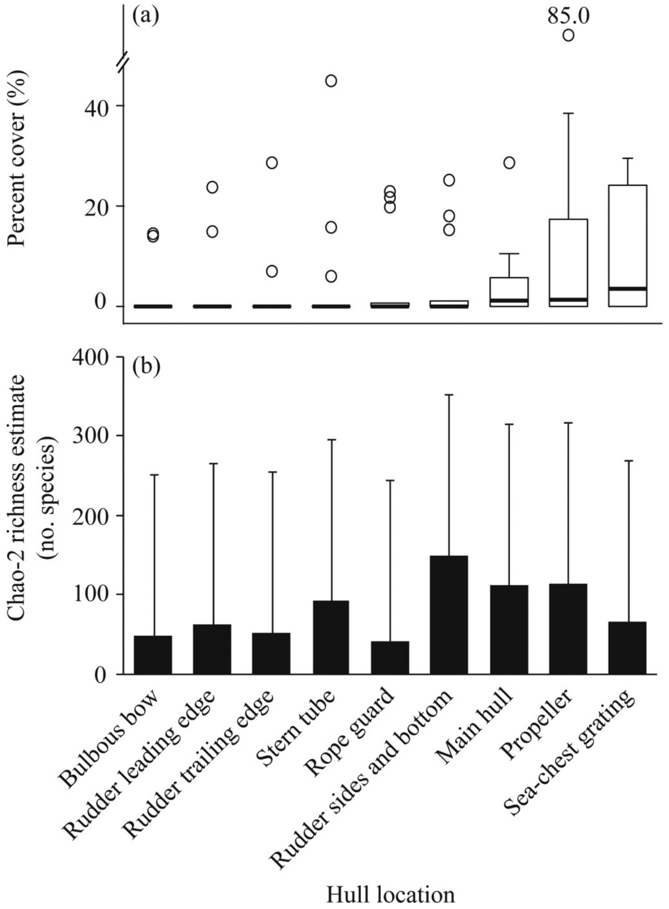
This study provides the first quantitative, comparative assessment of two potent transport vectors of NIS (i.e., hull fouling and ballast water) on the same vessels and is the first to examine fouling assemblages transported on hulls of vessels operating in an Arctic environment. Results from this study indicate that both hull fouling and ballast water are active vectors for delivering marine species to the Canadian Arctic. Hull fouling, however, appears to be the more important vector for delivery of NIS. While we did not find significant differences in total PP and CP for NIS between vectors within the same vessels, likely owing to the small

Fig. 3. Correlations between colonization pressure (solid circles) and total propagule pressure and between nonindigenous species (NIS) colonization pressure and total NIS propagule pressure (open circles) for hull fouling (left panels) and ballast water (right panels) assemblages transported per vessel. All data are log-transformed. Asterisks denote significance at 0.05.



sample size (n = 4), both nonindigenous total PP and nonindigenous CP were significantly higher for hull fouling than for ballast water when comparing vectors across vessels (n = 45). Additionally, a significant positive relationship between nonindigenous CP and nonindigenous total PP for hull fouling indicates a great potential for high-risk introduction events that involve many NIS, with most or all of them occurring in high abundance. In contrast, the absence of such a relationship for ballast water suggests that the number of NIS (i.e., diversity) transferred could be low despite high total PP (i.e., abundance) of NIS. Recent studies that assessed introduction risk using the CP:total PP relationship have identified four relative risk scenarios: (*i*) high risk: high CP and high total PP; (*ii*) and (*iii*) moderate risk: low CP and high total PP or high CP and low total PP; and (*iv*) low risk: low CP and low total PP (Briski et al. 2014; Drake et al. 2014; Chan et al. 2015). Following this conceptual model, hull fouling (high CP and high total PP) generally poses higher introduction risk than ballast water (low CP and high total PP), though low risk scenarios (i.e., low CP and total PP) exist for both vectors. A number of factors including characteristics of source community, occurrence and severity of selective pressures during transportation, duration of transport, and the nature of the vector (see below) can influence the structure of entrained assemblages and therefore the relationship between CP and total PP (Briski et al. 2012, 2014; Chan et al. 2015).

Fig. 4. (*a*) Median percent cover of fouling presented as Tukey box–whisker plots and (*b*) mean Chao-2 species richness estimates (+95% CI) for underwater locations across all vessels. Value off the scale is indicated.



The discovery of live specimens belonging to six widespread nonindigenous barnacles — *Amphibalanus amphitrite*, *Amphibalanus eburneus*, *Amphibalanus improvises*, *Amphibalanus reticulatus*, *Austrominius modestus*, and *Balanus trigonus* — on vessels arriving at Churchill further underscores the importance of hull fouling as a vector for delivering NIS to the Canadian Arctic. It was not possible to determine the origin of these species because they have widespread distributions (Carlton et al. 2011), and individuals could have accumulated on a ship's hull from different sources over time. These species were found on vessels that had travelled to Temperate North Atlantic, Temperate South Africa, Temperate South America, Tropical Atlantic, and West Indo-Pacific bioregions, demonstrating their ability to survive on hull surfaces during transoceanic voyages to high-latitude waters despite extensive longitudinal, latitudinal, and environmental changes. This finding appears to provide the first record of temperate fouling NIS surviving transit to an Arctic port, supporting previous risk assessments that identified *Amphibalanus improvises* and *Balanus trigonus* as risky NIS with potential to invade the Canadian Arctic because they have established populations at global ports directly connected to Churchill via shipping (Chan et al. 2012, 2013). *Amphibalanus amphitrite*, *Amphibalanus eburneus*, *Amphibalanus improvises*, and *Austrominius modestus* could potentially survive if introduced into Churchill based on their known thermal and salinity tolerances (Fofonoff et al. 2003; CABI 2014). If successfully established, they may compete with native species for food and space, alter community structure, and (or) cause changes in physical and chemical attributes of invaded habitats (Fofonoff et al. 2003; CABI 2014). In particular, *Amphibalanus improvises* and *Austrominius modestus* are considered high-impact NIS with ecological impact scores of four and three, respectively, in the four-point threat scoring system of Nature Conservancy's Global Marine Invasive Species Database owing to their abilities to disrupt multiple species and ecosystem processes with wide abiotic influences (Molnar et al. 2008). Temperate fouling NIS have also been found alive after long voyages to sub-Antarctic and Antarctic environments, highlighting the potential for transferring NIS on vessel hulls from temperate to

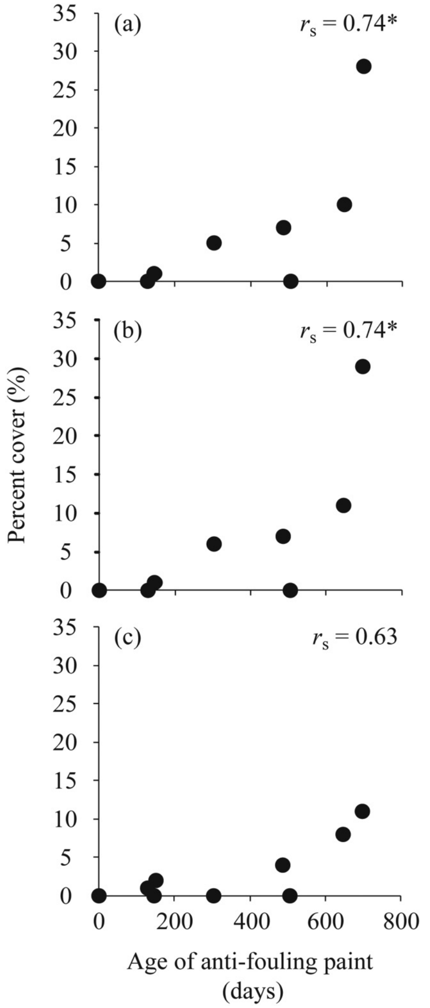


Fig. 5. Correlations between (*a*) overall percent cover, (*b*) hull percent cover, and (*c*) niche percent cover and age of antifouling paints (days since application). Asterisks denote significance at 0.05.

polar regions (Lewis et al. 2006; Lee and Chown 2009). In comparison, no temperate NIS capable of surviving environmental conditions in Churchill were found in ballast water. We observed a few Arctic NIS not previously reported from the Canadian Arctic in ballast samples, though it is possible that they are present, but not detected, in the region.

Operational features of hull fouling and ballast water could contribute to the relative importance of the vectors in transferring marine species. Fouling taxa can attach to hull surfaces at any time, most typically when vessels are in port, whereas ballast-mediated organisms are taken on board only when vessels load ballast (Hewitt et al. 2009). Greater nonindigenous total PP and nonindigenous CP observed for hull fouling than ballast water assemblages could result from the fact that vessels visited a number of global ports prior to Churchill, thereby exposing their hulls to a menagerie of species from a wide variety of source communities. In contrast, each vessel took up ballast water only at one or two source ports, thereby limiting the sources and diversity of organisms loaded. Additionally, we found relatively complex assemblages composed of benthic, sessile, and mobile taxa on vessel hulls. Sessile taxa, such as bivalves and cirripedes, can withstand high water velocities and provide structural habitat as well as protection for mobile organisms against sheer forces, thereby enhancing species diversity (Davidson et al. 2009; Clarke Murray et al. 2012). Conversely, we observed mainly holoplankton (e.g., copepods and rotifers) and planktonic larvae of benthic species (e.g., gastropods) in ballast water. We recognize that interior surfaces of sea-chest and ballast sediment may increase CP and total PP associated with hull fouling and ballast water, respectively (Coutts and Dodgshun 2007; Briski et al. 2011); however, we were not able to evaluate the importance of these subvectors in this study. In addition, one should be mindful that after arriving at Churchill, hull-borne organisms must be dislodged or reproduce to be introduced, thus the actual total PP and CP — including nonindigenous total PP and nonindigenous CP — released into the port environment are extremely difficult to quantify. In contrast, ballast water is far more straightforward, as almost all individuals carried in ballast water will be discharged into the harbour. Considering the volume of water released into Churchill, ballast water discharge may introduce substantial total PP and CP into the receiving environment. The potential for introducing ballast-mediated NIS, however, appears rather low owing to low nonindigenous total PP and nonindigenous CP found in ballast water of sampled ships.

Current management regimes for hull fouling and ballast water could also influence the relative role of the vectors by altering survivorship of organisms during transport. It is often assumed that organisms transported on ships' hulls have lower survivorship than those in ballast water because fouling taxa are directly exposed to the ambient environment and can experience extreme wave turbulence and fluctuations in water temperature and salinity during transoceanic voyages (Davidson et al. 2008; Hewitt et al. 2009). Conversely, organisms in ballast tanks are relatively protected from the external environment, though they may suffer high mortality within tanks owing to starvation, predation, light and oxygen limitation, or toxicity associated with antifouling applications (Hewitt et al. 2009). Nevertheless, a rather high fouling cover (10%–28%) was found on certain vessels, suggesting that existing antifouling practices are not sufficient to manage hull fouling. Although the International Maritime Organization (IMO) has introduced Guidelines for the Control and Management of Ships' Biofouling to Minimise the Transfer of Invasive Species (IMO 2011), hull maintenance remains a voluntary practice in Canada, carried out by vessel owners with the aim of reducing hydrodynamic drag and fuel consumption. On the other hand, all ballast water originating from foreign sources was exchanged mid-ocean, as required by Canada's mandatory ballast water management regulations (Government of Canada 2006). Ballast water exchange replaces coastal water loaded at ports with oceanic water, purging most coastal organisms and killing remaining ones via osmotic shock (Bailey 2015). The procedure is documented as 80%–100% effective in removing original coastal organisms (Bailey 2015). This may further contribute to the relatively low nonindigenous total PP and nonindigenous CP observed in ballast water, while total PP remained high, possibly due to the presence of oceanic species picked up during exchange.

While we could not contrast the abundance and diversity of species actually released and established for hull fouling versus ballast water in this study, previous work has suggested that the former is a more prevalent vector than the latter in a number of coastal ecosystems. Consistent with our results, hull fouling has also been implicated in a greater number of established NIS than ballast water in coastal regions of Antarctica (Lewis et al. 2003; Lee and Chown 2009), Australia and New Zealand (Hewitt et al. 2009), Brazil (Farrapeira et al. 2011), the North Sea (Gollasch 2002), and California in the United States of America (Williams et al. 2013). In Canada, however, ballast water is considered a stronger vector than hull fouling in terms of total PP and CP transported to the Atlantic and Pacific coasts (Sylvester et al. 2011). Ballast water, rather than hull fouling, is also considered the dominant transfer vector of NIS to the Great Lakes because of the salinity barrier imposed on fouling organisms (Sylvester and MacIsaac 2010).

Future changes in shipping activities are expected to alter the relative importance of hull fouling and ballast water in the Canadian Arctic. Over 25 large-scale mineral, offshore oil and gas, offshore energy, and infrastructure development projects have been planned for the region, some of which may be operational by 2020 (Gavrilchuk and Lesage 2014). These projects would lead to about 433 additional shipments per year, dramatically increasing shipping traffic in Canada's North from the current level of 599 arrivals per year (Chan et al. 2013; Gavrilchuk and Lesage 2014). Bulk carriers (190 000 deadweight tonnes) proposed for these projects are two to six times larger than the current fleet and would be discharging between 70 000 and 200 000 m^3 of ballast per shipment, which is 10 to 28 times greater than the current volume of discharge per vessel in Canadian Arctic waters (Stewart et al. 2012; Chan et al. 2013; Gavrilchuk and Lesage 2014). While the potential for both hull- and ballast-mediated transfers of NIS will clearly increase as a result of these proposed developments, the risk for the latter may increase to a greater extent than the former. Larger volume of ballast water carried by such vessels will likely lead to a proportional increase in total PP and CP of ballast-mediated organisms transferred, though the elevated risk could be mediated if the IMO Ballast Water Management Convention entered into force, requiring ships to manage ballast using treatment technologies to meet a numeric performance standard (IMO 2004). In contrast, greater wetted surface area does not necessarily result in a direct increase in total PP and CP of fouling organisms transported on hulls because surface area of fouling "hot spots" like the propeller and sea-chest will remain low, typically no more than 5% of total wetted surface area of vessels.

Identifying factors that may influence total PP and CP associated with hull fouling and ballast water can improve our ability to manage these vectors. Within individual vessels, we found that fouling (i.e., total PP) was not uniformly distributed across the hull, with sea-chest gratings and propellers tending to have higher fouling cover than other underwater vessel locations. CP, however, did not vary significantly across locations. This finding is generally consistent with a number of studies in which niche areas were found more heavily fouled than the main hull (e.g., Coutts and Taylor 2004; Davidson et al. 2009; Sylvester and MacIsaac 2010). Fouling extent also varied across vessels. We found a significant positive correlation between percent cover of fouling and age of antifouling paint. The influence of antifouling paint age, however, was observed for overall and main hull fouling, but not for niche area fouling. In general, vessels with older antifouling paint support richer and denser fouling assemblages than those that are recently painted because effectiveness of antifouling paint decreases with time (Davidson et al. 2009; Sylvester et al. 2011). However, antifouling paints are usually not applied properly on niche areas because they are difficult to access during paint application, and efficacy is often compromised because they age prematurely owing to extreme turbulence (e.g., bulbous bow) or remain inactive owing to insufficient water flow (e.g., rope guard) (Coutts and Taylor 2004). As a result, fouling extent may not be related to age of antifouling paint at these locations (Clarke Murray et al. 2011). The high occurrence of nonindigenous barnacles in niche areas of sampled vessels provides additional evidence that these locations are vulnerable to NIS fouling. None of the other variables examined, including age of antifouling paint, total port residence time, and number of bioregions visited, were related to total PP, CP, nonindigenous total PP, and nonindigenous CP for hull fouling assemblages. Previous studies have found vessels that spent more time in ports accumulated greater fouling because longer residency provides greater opportunity for organisms to colonize hull surfaces (Davidson et al. 2009; Sylvester and MacIsaac 2010; Sylvester et al. 2011). Sylvester et al. (2011) also observed a positive relationship between diversity of fouling assemblages and the number of bioregions visited by vessels, possibly as a result of greater exposure to a wide variety of biological communities. The absence of a significant relationship between most fouling variables and vessel characteristics in this study may be due to the small sample size. Alternatively, the effects of these variables on fouling extent could be obscured by Churchill's Arctic environment, particularly the presence of sea ice. Ice scouring removes or negatively impacts fouling assemblages on vessels and plays a crucial role in determining fouling extent in high-latitude waters (Lee and Chown 2009; Sylvester et al. 2011). Data from Canadian Ice Services (2014) indicate that sea ice was present in the Hudson Strait and Labrador Sea during this study period; thus, ice scouring is possible. By contrast, total PP and CP transported in ballast water were negatively related to age of ballast water (see Chan et al. 2014).

Because of the nature of the transport vectors, substantially different sampling methods were used to collect samples from hulls and ballast water. We followed standard methods, ensuring each vector was surveyed to the best extent possible. Differences in methodologies may, however, lead to biases in results. For example, ~10 replicates were collected across different parts of the hull to cover the range of habitats that may support fouling species. In contrast, only one ballast water sample was collected from one tank per ship because repeated vertical plankton hauls are adequate in collecting invertebrates from the entire water column inside a ballast tank (Gray et al. 2007), and the collected sample is expected to be representative of all ballast water on board (see Materials and methods). Indeed, matching observed and estimated (Chao-1) species richness values for ballast water assemblages suggests that sampling effort is adequate for characterizing the full extent of biodiversity in ballast water, whereas discrepancy between observed and estimated (Chao-2) richness indicates the opposite for hull fouling. Additionally, sample size for hull fouling (n = 13 ships) was smaller than that for ballast water (n = 32 ships) owing to constraints imposed by ships' operations, weather conditions, schedules of SCUBA divers, and cost. Thus, ballast water sampling may have been more likely to detect the array of intervessel biodiversity differences than sampling conducted on vessel hulls.

The Arctic is one of the least invaded ecosystems on earth. Arctic coastal environments are, however, under unprecedented threats from NIS owing to a combination of climate change, resource development, and the growth of Arctic shipping (Miller and Ruiz 2014). This study reveals that diverse marine communities are arriving at the Canadian Arctic via vessel hull fouling and the discharge of ballast water. Hull fouling appears to be the more prominent transport vector of NIS, delivering a number of viable, widespread nonindigenous cirripede species to the region. Some of these NIS have the ability to tolerate current environmental conditions in Churchill and may have adverse impacts on resident communities if successfully established. Future climate warming may increase the potential of survival and establishment of other ship-mediated NIS. The relative importance of hull fouling and ballast water as transport vectors of NIS may vary in response to changes in shipping patterns, vector management regimes, and environmental conditions; thus, attention should be given to both transport vectors.

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Appendix A

Appendix Tables A1 and A2 appear on the following pages.

Table A1. List of invertebrate taxa observed in hull fouling assemblages of vessels arriving at the Port of Churchill, Manitoba.

Taxon	Occurrence (%)	Mean abundance (individuals·ship^{-1})	Live specimen	Category	Reference
Acari					
Halacaridae	1 (7.7%)	8 907		UK	
Amphipoda					
Calliopius laeviusculus	1 (7.7%)	555	Y	HB	Steele 1961; Bousfield 1973; Stewart and Lockhart 2005
Crassicorophium bonellii	1 (7.7%)	59		AR*	Bousfield 1973; EOL 2014; Sirenko et al. 2014
Gammaracanthus loricatus	1 (7.7%)	538	Y	HB	Steele 1961; Atkinson and Wacasey 1989; Stewart and Lockhart 2005
Gammarus oceanicus	1 (7.7%)	5 731	Y	HB	Atkinson and Wacasey 1989; Stewart and Lockhart 2005; Goldsmit et al. 2014
Gammarus setosus	5 (23.1%)	5 895±711		HB	Atkinson and Wacasey 1989; Stewart and Lockhart 2005; Goldsmit et al. 2014
Gammarus sp.	1 (7.7%)	187	Y	UK	
Jassa marmorata	1 (7.7%)	5		AR*	Bousfield 1973; EOL 2014; Sirenko et al. 2014
Bivalvia					
Bivalvia (juveniles)	3 (23.1%)	4 790±1 797	Y	UK	
Chamidae	2 (15.4%)	3 400±1 295		UK	
Corbulidae	1 (7.7%)	10		UK	
Hiatella arctica	2 (15.4%)	3 472±1 326	Y	IN	Atkinson and Wacasey 1989; Stewart and Lockhart 2005; Goldsmit et al. 2014
Musculus sp.	1 (7.7%)	44		UK	
Myidae	1 (7.7%)	6 702		UK	
Mytilidae	5 (38.5%)	963±513		UK	
Mytilus edulis	1 (7.7%)	198		HB	Atkinson and Wacasey 1989; Stewart and Lockhart 2005; Goldsmit et al. 2014
Mytilus sp.	2 (15.4%)	2 569±996		UK	
Chironomidae				UK	
Chironomidae	1 (7.7%)	306		UK	
Cirripedia					
Amphibalanus amphitrite	5 (38.5%)	112 859±69 678	Y	NA*	Newman and Ross 1976; Fofonoff et al. 2003
Amphibalanus eburneus	1 (7.7%)	530	Y	NA*	Newman and Ross 1976; Carlton et al. 2011; Fofonoff et al. 2003
Amphibalanus improvisus	3 (23.1%)	11 396±3 511	Y	NA*	Henry and McLaughlin 1975; Fofonoff et al. 2003

Table A1 (*continued*).

Taxon	Occurrence (%)	Mean abundance (individuals·ship^{-1})	Live specimen	Category	Reference
Amphibalanus reticulatus	3 (23.1%)	11 432±5 373	Y	NA*	Newman and Ross 1976; Fofonoff et al. 2003
Amphibalanus sp. 1	1 (7.7%)	78 371		UK	
Amphibalanus sp. 2	2 (15.4%)	62		UK	
Austrominius modestus	1 (7.7%)	2 005	Y	NA*	Newman and Ross 1976; CABI 2014; OBIS 2014
Balanidae sp. 1	8 (61.5%)	130 559±62 593	Y	UK	
Balanidae sp. 2	1 (7.7%)	54	Y	UK	
Balanoidea sp.	1 (7.7%)	155 563	Y	UK	
Balanus trigonus	2 (15.4%)	371 564±98 584	Y	NA*	Newman and Ross 1976; CABI 2014; OBIS 2014
Conchoderma auritum	1 (7.7%)	1 074	Y	NA*	OBIS 2014
Conchoderma virgatum	1 (7.7%)	139	Y	NA*	OBIS 2014
Fistulobalanus sp.	1 (7.7%)	36 319		UK	
Megabalanus cf. *spinosus*	1 (7.7%)	10 702		NA*	Henry and McLaughlin 1986
Megabalanus cf. *tintinnabulum*	1 (7.7%)	6 354		NA*	Darwin 1851; Pilsbry 1916
Megabalanus coccopoma	2 (15.4%)	295 297±115 396		NA*	Fofonoff et al. 2003
Megabalanus sp. 1	1 (7.7%)	1 882		UK	
Megabalanus sp. 2	1 (7.7%)	1 556 885		UK	
Megabalanus sp. 3	3 (23.1%)	122 012±57 591		UK	
Newmanella sp.	1 (7.7%)	57 861		UK	
Perforatus sp.	2 (15.4%)	310 445±121 268	Y	UK	
Cladocera					
Acantholeberis curvirostris	1 (7.7%)	2 164		NA*	EOL 2014
Alona sp.	1 (7.7%)	59			
Copepoda					
Acartia hudsonica	3 (23.1%)	5 438±1 412		CA	Roff and Legendre 1986; OBIS 2014
Acartia longiremis	1 (7.7%)	139		HB	Shih et al. 1971; Roff and Legendre 1986; Stewart and Lockhart 2005
Acartia sp.	3 (23.1%)	3 240		UK	
Calanoida	4 (30.8%)	6 671±2 945		UK	
Calanus finmarchicus	1 (7.7%)	36		HB	Shih et al. 1971; Grainger 1963; Roff and Legendre 1986
Calanus sp.	1 (7.7%)	3 889		UK	
Centropages sp.	1 (7.7%)	563		UK	
Cyclopoida	3 (23.1%)	560±231		UK	
Dactylopusia vulgaris	1 (7.7%)	45		HB	Shih et al. 1971; Stewart and Lockhart 2005
Ectinosoma sp.	1 (7.7%)	4		UK	
Harpacticoida	1 (7.7%)	4		UK	
Harpacticus sp.	1 (7.7%)	45		UK	
Laophontidae sp.	1 (7.7%)	1 585		UK	
Mesochra sp.	1 (7.7%)	5 108		UK	
Metridia lucens	1 (7.7%)	15 323		HB	Shih et al. 1971; Stewart and Lockhart 2005
Microsetella norvegica	3 (23.1%)	3 369±1 509	Y	HB	Shih et al. 1971
Oithona similis	3 (23.1%)	4 670±1 562		HB	Shih et al. 1971; Roff and Legendre 1986
Oncaea sp.	1 (7.7%)	632		UK	
Paradactylopodia brevicornis	1 (7.7%)	139		CA	Shih et al. 1971
Paronychocamptus huntsmani	3 (23.1%)	11 037±3 250		NA*	Shih et al. 1971; OBIS 2014; WoRMS 2014
Pseudcalanus sp.	2 (15.4%)	220±77		UK	
Pseudobradya sp.	1 (7.7%)	145		UK	
Sarsamphiascus minutus	1 (7.7%)	5 118		CA	Shih et al. 1971
Schizopera clandestina?	2 (15.4%)	72±23		NA*	EOL 2014; WoRMS 2014
Tisbe furcata?	1 (7.7%)	561		HB	Shih et al. 1971; Stewart and Lockhart 2005
Zaus sp.	2 (15.4%)	111±11		UK	
Echinodermata					
Phoronida	1 (7.7%)	4 265		UK	
Gastropoda					
Patellogastropoda	1 (7.7%)	125		UK	
Nematoda					
Camacolaimus sp.	1 (7.7%)	4		UK	
Chromadoridae	1 (7.7%)	59		UK	
Chromadorina sp.	1 (7.7%)	10 171		UK	
Chromadorita sp.	1 (7.7%)	96		UK	
Dichromadora sp.	1 (7.7%)	19		UK	
Geomonhystera sp.	2 (15.4%)	47±9		AR*	R. Fisher, personal communication, 2009; OBIS 2014
Ironidae	1 (7.7%)	8 848		UK	
Leptolaimoides sp.	1 (7.7%)	12		UK	
Oncholaimus sp.	1 (7.7%)	12		UK	
Prochromadora orleji	1 (7.7%)	202 712		NA*	EOL 2014; OBIS 2014
Prochromadora sp.1	1 (7.7%)	40 387		UK	
Prochromadora sp.2	2 (15.4%)	6 538±2 537		UK	

Table A1 (*concluded*).

Taxon	Occurrence (%)	Mean abundance (individuals·ship^{-1})	Live specimen	Category	Reference
Ostracoda					
Cytherocopina	1 (7.7%)	1 113		UK	
Polychaeta					
Exogone sp.	1 (7.7%)	125		UK	
Phyllodoce sp.	1 (7.7%)	27		UK	
Phyllodocidae	2 (15.4%)	2 402±731		UK	
Spionidae	1 (7.7%)	70		UK	

Note: Frequency of occurrence in 13 vessels, mean abundance (±SE) when present, presence of live specimens (Y = yes), taxa category, and references used are also included. Question marks (?) denote taxonomic identification with uncertainty. HB = Hudson Bay, CA = Canadian Arctic, AR = Arctic, NA = non-Arctic, and UK = unknown. Asterisks indicate taxa considered as nonindigenous to Churchill in this study.

Table A2. List of invertebrate taxa found in ballast water of vessels arriving at the Port of Churchill, Manitoba.

Taxon	Occurrence (%)	Mean abundance (individuals·ship^{-1})	Category	Reference
Acari				
Acari	2 (6.3%)	26 096±3 633	UK	
Amphipoda				
Themisto gaudichaudi	7 (21.9%)	59 470±7 488	CA	Shih et al. 1971; Stewart and Lockhart 2005
Themisto sp.	1 (3.1%)	9 212	UK	
Bivalvia				
Bivalvia (juveniles)	7 (21.9%)	172 524±41 328	HB	Water samples
Chaetognatha				
Sagittidae	1 (3.1%)	10 753		
Cirripedia				
Cirripedia (larvae)	9 (28.1%)	632 893±300 133	HB	Water samples
Cladocera				
Cladocera	1 (3.1%)	150 028		
Daphnia sp.	1 (3.1%)	19 380		
Copepoda				
Acartia clausi	3 (9.4%)	3 854 453±887 656	HB	Shih et al. 1971; Roff and Legendre 1986; Stewart and Lockhart 2005
Acartia hudsonica	2 (6.3%)	40 198 578±17 778 782	CA	OBIS 2014
Acartia sp.	1 (3.1%)	932 957	UK	
Calanoida	2 (6.3%)	52 396±34 815	UK	
Calanus finmarchicus	1 (3.1%)	2 321 454	HB	Willey 1931; Grainger 1963; Roff and Legendre 1986
Calanus glacialis	3 (9.4%)	8 879 446±3 854 319	HB	Shih et al. 1971; Grainger 1963; Grainger 1968
Calanus sp.	2 (6.3%)	34 553	UK	
Centropages hamatus	1 (3.1%)	1 079 341	HB	Shih et al. 1971; Boxshall 2014
Centropages sp.	1 (3.1%)	1 892 957	UK	
Centropages typicus	1 (3.1%)	524 587	AR*	Shih et al. 1971; OBIS 2014
Clausocalanus mastigophorus	2 (6.3%)	306 293±38 702	HB	Shih et al. 1971; Stewart and Lockhart 2005
Copepoda	2 (6.3%)	9 217±848	UK	
Cyclopoida	1 (3.1%)	34 176	UK	
Ectinosoma sp.	1 (3.1%)	8 830	UK	
Euterpina acutifrons	2 (6.3%)	1 499 803±11 958	CA	OBIS 2014
Heterolaophonte ströemi	1 (3.1%)	22 891	AR*	Shih et al. 1971; Kotwicki 2002
Metridia lucens	1 (3.1%)	208 188	HB	Shih et al. 1971; Stewart and Lockhart 2005
Microsetella norvegica	12 (37.5%)	630 804±138 881	HB	Water samples; Shih et al. 1971
Nitokra lacustris	1 (3.1%)	739 393	NA*	Rhodes 2003; WoRMS 2014
Oithona atlantica	1 (3.1%)	14 935 778	CA	WoRMS 2014
Oithona similis	23 (71.9%)	11 351 661±3 678 529	HB	Water samples; Shih et al. 1971; Roff and Legendre 1986
Oncaea sp.	8 (25.0%)	407 633±197 929	UK	
Paracalanus parvus	5 (15.6%)	4 373 285±1 105 744	HB	Shih et al. 1971
Pseudocalanus newmani	3 (9.4%)	690 386±124 622	CA	Stewart and Lockhart 2005
Pseudocalanus sp.	2 (6.3%)	418 046±140 494	UK	
Temora longicornis	2 (6.3%)	5 180 515±995 940	CA	Shih et al. 1971
Tisbe furcata?	1 (3.1%)	25 632	HB	Water samples; Shih et al. 1971; Stewart and Lockhart 2005
Echinodermata				
Echinodermata	1 (3.1%)	9 309	UK	
Ophiuroidea	1 (3.1%)	133 590	UK	
Gastropoda				
Calyptraeidae	3 (9.4%)	34 686±3 759	UK	
Cerithiidae	1 (3.1%)	19 710	UK	
Gastropoda	2 (6.3%)	12 156±712	UK	
Heterobranchia	5 (15.6%)	1 679 009±439 589	UK	
Rissoidae	1 (3.1%)	8 700	UK	

Table A2 (*concluded*).

Taxon	Occurrence (%)	Mean abundance (individuals·ship^{-1})	Category	Reference
Isopoda				
Gnathiidae	2 (6.3%)	30 464±5 524	UK	
Nematoda				
Ascolaimus sp.	1 (3.1%)	67 830	AR*	R. Fisher, personal communication, 2009; EOL 2014; OBIS 2014
Axonolaimidae	1 (3.1%)	78 840	AR*	R. Fisher, personal communication, 2009; EOL 2014; Sirenko et al. 2014
Chromadoridae	2 (6.3%)	32 760±1 665	UK	
Comesomatidae	1 (3.1%)	13 366	UK	
Daptonema tenuispiculum	2 (6.3%)	159 270±3 682	NA*	OBIS 2014
Geomonhystera sp.	4 (12.5%)	189 361±22 165	AR*	R. Fisher, personal communication, 2009; OBIS 2014
Omicronema sp.	1 (3.1%)	42 720	UK	
Prochromadora sp.	4 (12.5%)	81 436±8 835	UK	
Polychaeta				
Hesionidae	1 (3.1%)	12 795	UK	
Pholoididae	1 (3.1%)	27 927	UK	
Polydora sp.	2 (6.3%)	62 465±11 266	UK	
Spionidae	5 (15.6%)	204 804±58 053	UK	
Streblospio sp.	1 (3.1%)	129 035	UK	
Rotifera				
Rotifera	4 (12.5%)	16 893±725	UK	
Synchaetidae	4 (12.5%)	23 108 818±8 149 955	HB	Water samples

Note: Frequency of occurrence in 32 vessels, mean abundance (±SE) when present, taxa category, and references used were also included. Question mark (?) denotes taxonomic identification with uncertainty. Taxa present in port water samples were considered native to Hudson Bay. Category follows Table A1. Asterisks indicate taxa considered nonindigenous to Churchill in this study.

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